UNIVERSITY OF ALBERTA

THE IMPACT OF RADIOTELEMETRY ON MALLARD REPRODUCTIVE SUCCESS

by

RICHARD MICHAEL CHABAYLO

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The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled THE IMPACT OF RADIOTELEMETRY ON MALLARD REPRODUCTIVE SUCCESS submitted by RICHARD MICHAEL CHABAYLO in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

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Abstract

This study investigated the question: why do female dabbling ducks suffer such apparently high total brood loss when fitted with backpack radio transmitters? Using mallards, I tested the impact of radio backpacks on a number of variables, including incubation constancy, egg cooling, and hatching success of hens in the wild and in captivity. In the latter group the following variables were also considered: neonate body reserves, growth, and survival. Finally, I documented post-hatch behaviour and body weight changes in radio-marked captive females.

Post-handling absence, egg cooling, and nest desertion were higher for radio-marked than unmarked mallards in the wild. Egg hatchability for all mallards in this study was high (>90%) and appeared little affected by prolonged exposures to moderate cooling temperatures. Duckling survival for radio-marked hens in captivity was also high (>90%), comparable to unmarked hens. The majority of duckling deaths occurred during the first week post-hatch. Viability appeared to be influenced by embryonic cooling and hatch weight: heavy ducklings from eggs incubated naturally survived better than light ducklings from eggs cooled experimentally. There are two potential explanations for this: (1) larger ducklings hatched with proportionately larger yolk sacs, containing relatively more endogenous reserves, and (2) prolonged embryonic cooling resulted in lower lipid levels and decreased tissue maturity (as indicated by higher water content) of neonates. Embryonic cooling caused the resulting hatchlings to grow more slowly (especially for females), suggesting that reduced yolk and body reserves may be the cause.

Female post-hatch behaviour and weight gain were altered by radio-marking. Those with backpacks spent significantly less time on the water and more time preening. Given an unlimited nutritional diet and security from predators, captive females spent considerably more time in alert behaviour (ca. 22%) than feeding (ca. 2%) during the first 2 weeks post-hatch. The rate of weight gain was significantly lower for those with radio transmitters, as was body weight at the end of the summer. Transmitters affected the body weight of heavy hens more than that of light hens. Using body weight as an indicator of endogenous reserves, it would appear that heavier hens can withstand a greater weight loss than lighter individuals; whereas the latter are near a critical level of reserves and must increase their caloric intake to compensate. I discuss the implications of these data and how the subtle effects found here are additive, resulting in lower reproductive success among radio-marked female mallards. Altenative transmitter designs should be considered.

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Table of contents

Chapter — Page

I. INTRODUCTION 1
LITERATURE CITED 5

II. THE EFECTS OF RADIO-MARKING ON PRE- AND POST-HATCH BEHAVIOUR OF FEMALE MALLARDS: IMPLICATIONS FOR HATCHING SUCCESS AND DUCKLING SURVIVAL 7
INTRODUCTION 7
STUDY AREA AND METHODS 10
Capture and radio-marking procedure 10
Egg temperatures and incubation constancy 11
Egg cooling and hatchability 12
Survival of captive ducklings 13
Brood rearing behaviour 13
Statistical analyses 15
RESULTS 16
Nest desertion 16
Post-handling nest attentiveness 18
Egg hatchability 18
Duckling survival 23
Time-activity budgets of brood rearing females 27
DISCUSSION 32
Frequency of nest abandonment 32
Nest attentiveness and egg cooling 33
Hatchability of cooled eggs 34
Duckling survival 36
Time-activity budgets 39
LITERATURE CITED 41

III. NEONATE BODY RESERVES: THE INFLUENCE OF EGG COOLING AND BODY SIZE 49
INTRODUCTION 49

Chapter Page

STUDY AREA AND METHODS 51
Duckling body reserves 51
Duckling growth 52
Statistical analyses 53
RESULTS 53
Influence of egg cooling on neonate body reserves 53
Liver 53
Yolk sac 54
Carcass 61
Whole duckling 61
Relationship between body components and neonate mass 64
Neonate growth 64
DISCUSSION 67
Influence of egg cooling on neonate body reserves 67
Relationship of body components to neonate mass 72
Neonate growth rates 75
LITERATURE CITED 78

IV. THE INFLUENCE OF RADIO BACKPACKS ON WEIGHTS OF FEMALE MALLARDS DURING BROOD REARING: IMPLICATIONS FOR DUCKLING SURVIVAL 83
INTRODUCTION 83
STUDY AREA AND METHODS 84
Statistical analyses 85
RESULTS 86
DISCUSSION 91
Influence of radio backpacks on changes in hen weight 91
Implications for recruitment studies 93
Implications for female survival 95
Alternatives to current techniques 96
LITERATURE CITED 98

V. CONCLUDING DISCUSSION 104
LITERATURE CITED 109
Appendix I 112

Chapter Page

Appendix II 113

List of Tables

Table		Page
II-1:	Clutch size and nesting success of wild mallard hens trapped on the nest in late incubation (estimated day 22). The birds were either fitted with a dummy radio transmitter (radio-marked) or handled only (unmarked)	17
II-2:	Incubation behaviour of radio-marked (n=11) and unmarked (n=9) wild mallard hens after being trapped on the nest late in incubation	19
II-3:	Egg and ambient temperatures (°C) during absences from the nest for radio-marked (n=11) and unmarked (n=9) wild mallard hens in late incubation	20
II-4:	Incubation behaviour of radio-marked (n=16) and unmarked (n=12) captive mallard hens after being trapped on the nest and handled late (day 22) in incubation	21
II-5:	Hatchability estimates for successful (hatched one or more eggs) wild and captive mallard hens, both radio-marked and unmarked	22
II-6:	Hatchability of artificially incubated mallard eggs, cooled experimentally at three temperatures and for three durations on the 22nd day of incubation	24
II-7:	Hatchability of mallard eggs from the nests of captive hens (n=36) after being cooled experimentally (on the 22nd day of incubation) for a combination of two temperatures and two durations	25
II-8:	Number of ducklings dying during brood rearing by captive mallard hens. Ducklings were classified as either light (<33 g) or heavy (>33 g), and whether they were cooled experimentally as 22-day-old embryos or incubated naturally (control)	28
II-9:	A summary of variables obtained from behavioural observations of captive radio-marked and unmarked mallard hens during early brood rearing	29
II-10:	The percentage (mean±SE) of total observation hours conducted during each of five intervals of the day for captive radio-marked and unmarked mallard hens during early brood rearing	30
III-1:	Summary of analyses for the composition of four mallard duckling components (liver, yolk sac, carcass, whole duckling) in relation to egg cooling, size, and sex	56
III-2:	Body component variables for 12-hour-old mallard ducklings that were either cooled experimentally (15°C-12h and 10°C-12h)on the 22nd day of incubation, or not (control)	58
III-3:	Summary of log-log regression analyses of components (Y) on duckling body weight (X) for neonate mallards	65
III-4:	Growth variables (mean±SE) of male and female mallard ducklings from uncooled eggs (control) and those from eggs cooled on the 22nd day of incubation	66
III-5:	Growth variables (mean±SE) of male and female mallard ducklings categorized as either light (<33 g) or heavy (>33 g) at hatching	68
IV-1:	Mean (±SE) pre- and post-hatch body weights and absolute weight change of captive radio-marked and unmarkd female mallards	88

Table Page

IV-2: Mean (±SE) hatch dates and pre- and post-hatch body weights for light (<1000 g) and heavy (>1000 g) female mallards, either radio-marked or unmarked 90

List of Figures

Figure — Page

II-1 Cumulative survival over time for captive mallard ducklings, either from (A) broods of radio-marked or unmarked hens, (B) cooled or uncooled eggs, or (C) for those catagorized as either light (<33 g) or heavy (>33 g) at hatch 26

II-2: Percent of time spent by brood rearing female mallards, either radio-marked (n=20) or unmarked (n=20), in various behavioural activities 31

III-1: Content variables for the livers of mallard ducklings hatched from eggs either cooled on the 22nd day of incubation or not (control) 55

III-2: Content variables for the yolk sacs of mallard ducklings hatched from eggs either cooled on the 22nd day of incubation or not (control) 60

III-3: Content variables for the carcasses (lacking liver and yolk sac) of mallard ducklings hatched from eggs either cooled on the 22nd day of incubation or not (control) 62

III-4: Content variables of whole mallard ducklings hatched from eggs either cooled on the 22nd day of incubation or not (control) 63

IV-1: Mean weekly body weights (A) and absolute changes (B) for mallard females during brood rearing, either fitted with a radio backpack in late incubation (day 22) or left unmarked 87

IV-2: Mean body weights for heavy (>1000 g) and light (<1000 g) mallard females during and after brood rearing, either fitted with a radio backpack in late incubation (day 22) or not 89

I. INTRODUCTION

Declining North American duck populations have become the subject of considerable concern continent-wide (Reinecke 1982, Anderson and Batt 1983, CWS and USFWS 1986). The abundance of ducks, especially the larger species of dabbling ducks (Anatinae), has declined since the mid-1950's, when systematic population surveys began. The mallard (*Anas platyrhynchos*), most abundant and heavily harvested of all North American waterfowl, has declined from an estimated 12.9 million breeding birds in 1958 to a record low of 5.5 million in 1985 (CWS and USFWS 1986). A similar decline has been recorded in several other species of surface-feeding ducks, including the northern pintail (*Anas acuta*) which dropped from 10.1 million in 1956 to 2.5 million by 1989 (Calverley pers. comm. 1989).

Chronic drought, which began in the late 1970's on the northern Great Plains of Canada and the U.S., has exacerbated these declines in the last decade. This region, the prime breeding range for the majority of North American ducks (Bellrose 1976), is also the heart of cereal crop production in North America. Prior to and coincident with the drought, the fertile prairies and parklands of this region were highly modified by agriculture. Modern farming practices have led to accelerated rates of wetland drainage and destruction of critical upland nesting cover. Loss of nesting habitat continues especially in areas marginally suited to grain farming such as the edges of shrunken wetland basins (Boyd 1985). Diminished availability of upland habitat has forced predators of waterfowl (mammalian and avian) to intensify their foraging efforts in the remaining cover where upland nesting ducks are also forced to concentrate. Heavy predation (Cowardin et al. 1983) and excessive harvest (Trauger and Stoudt 1978, Couch and Boyd 1984, Jakimchuk and Sopuck 1987) has led to lowered productivity in these populations, reducing them to a fraction of their former levels. The population decline in upland nesting ducks is probably one of the more serious and certainly the

most widespread problem facing waterfowl managers in North America.

Although intensely debated, most researchers maintain that decreased productivity is the primary cause of the decline in duck populations (Hochbaum and Caswell 1978, Cowardin and Johnson 1979, Cowardin et al. 1985, Greenwood et al. 1988). There is a general concensus that waterfowl production can be affected by any of the following variables: (1) density of breeding birds, (2) nesting success, and (3) brood survival, but the magnitude of the latter is considered the key factor. Measurement of brood survival is essential for calculating recruitment from nesting data (Cowardin and Johnson 1979). Dzubin and Gollop (1972) concluded that brood survival was the single most important proximate factor determining fall population size of mallards in their study area on the Canadian parklands and prairies. Yet survival of ducklings from hatching to fledging remains poorly understood (Cowardin and Johnson 1979).

Counting the number of young in unmarked broods of ducks and estimating their age has been used traditionally to calculate survival. The number of ducklings in age-class III broods (Gollop and Marshall 1954) is considered a reliable index of recruitment because juveniles at this stage have survived most of the brood rearing period. However, Reed (1970) and Ball et al. (1975) emphasized that survival rate estimates for unmarked broods fail to account for instances in which all ducklings in a brood perish. As a result, methods using radiotelemetry were developed to relocate birds at will and to follow the fate of their broods in the field.

Techniques using radiotelemetry have revolutionized the study of many aspects of avian biology, having many advantages over strictly observational methods. For example, by periodically relocating radio-marked hens with broods during the post-hatch period, survival of young can be determined. Such studies, however, have raised a number of questions about the technique. Reed (1972) documented that 2 of 5 radio-marked black duck (*A. rubripes*) hens lost their entire brood within 6 days of

leaving the nest. Ringelman and Longcore (1982) found that at least 1 (4%) unmarked and 5 (63%) radioed black duck hens lost all their ducklings. While working with radio-marked northern pintails and gadwalls (*A. strepera*), Duncan (1986) recorded very high brood losses. 11 (73%) hens failing to fledge any ducklings, all being lost within 9 days of hatch. Studies using radio-marked mallard hens have had similar results. 13 (52%) hens lost their entire brood, with these losses accounting for 68% of all mortality (Talent et al. 1983), and 10 (37%) hens lost all their ducklings, explaining 60% of all losses (Orthmeyer 1987). Yarris (pers. comm. 1987) observed that only 2 of 23 (7%) radio-marked mallards fledged any ducklings at all. These studies provide evidence that total brood loss among radio-marked hens is very high, suggesting that the technique may be a contributing cause.

Early studies of duckling survival have established that most brood attrition, even that resulting in the loss of all ducklings, occurs during the first 2 weeks after hatching and is typical of many areas and duck species (Keith 1961, Dwernychuk 1968, McGilvrey 1969, Reed 1970, Bengston 1972, Dzubin and Gollop 1972, Ringelman and Longcore 1982, Talent et al. 1983). Although the causes of these early deaths are poorly understood, losses have been attributed usually to predation, starvation, drought conditions, and/or chilling during inclement weather. In addition, if females vary in their ability to rear broods successfully, or even if chance variations in survival are considered, some total brood mortality would be expected (Ball et al. 1975). However, brood survival studies using radio-equipped females have produced equivocal results; the broods of marked hens appear to suffer unusually high mortality. Could these results be an artifact of the method - forcing the hen to carry a radio transmitter? To answer this question it is necessary to evaluate the impact of the radio transmitter on the behaviour and physiology of the brood hen directly, and on that of her brood indirectly.

In the remaining chapters I focus on answering the question: is duckling survival influenced by the presence of a radio transmitter on the female parent? Chapter II

evaluates the effect of radio backpacks on the behaviour of mallard hens and how, as a result, their offspring may also suffer. In it I examine nest attentiveness, egg cooling and its influence on hatchability and duckling survival, and brood rearing behaviour. In Chapter III I consider the possibilty that radio-marking the hen may also have an impact on the neonates which hatch subsequently from eggs exposed to prolonged periods of cooling. I do this by investigating endogenous reserves and post-hatch growth of ducklings. Chapter IV deals with female body condition, and reports on the weight changes in hens after being fitted with a radio transmitter. The concluding discussion in Chapter V integrates the information of Chapters I to IV. I establish that (1) attachment of a radio transmitter to an incubating duck produces long-lasting effects on the hen, (2) duckling survival is both directly and indirectly influenced by radio-marking the female duck, (3) certain implications must be considered when employing radiotelemetry of the type described herein, as a tool for obtaining waterfowl recruitment estimates for management purposes.

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II. THE EFFECTS OF RADIO-MARKING ON PRE- AND POST-HATCH BEHAVIOUR OF FEMALE MALLARDS: IMPLICATIONS FOR HATCHING SUCCESS AND DUCKLING SURVIVAL

INTRODUCTION

Radiotelemetry is a technique that has given biologists the opportunity to collect data on a variety of avian behavioural and life history attributes. For these data to be meaningful, however, it is important to determine whether the characteristics measured are influenced by applying the technique, namely placing a transmitter on the individual to be studied (Giroux et al. 1990). The effects of radio packages on avian behaviour have been evaluated in a number of studies, primarily on game bird species (anseriforms and galliforms). The results varied from a small to a large impact, and are summarized as follows: temporary discomfort, preening, and preoccupation with the transmitter (Dwyer 1972, Gilmer et al. 1974, Morris and Black 1980), an aversion to water among ducks (Greenwood and Sargeant 1973, Gilmer et al. 1974, Perry 1981), reduced or altered foraging behaviour (Boag 1972, Perry 1981, Massey et al. 1988, Wanless et al. 1988), weight loss and feather wear (Schladweiler 1969, Greenwood and Sargeant 1973, Perry 1981), abnormal breeding behaviour (Ramakka 1972, Wanless et al. 1985, Massey et al. 1988), decreased reproductive success (Lance and Watson 1977, Herzog 1979, Erikstad 1979, Hines and Zwickel 1985), and decreased survival (Gilmer et al. 1974, Warner and Etter 1983, Small and Rusch 1985). These studies demonstrated clearly that (1) there is an adjustment period, lasting several days for most birds, during which the individual accommodates to the presence of the radio, and (2) others, failing to adjust fully, experience harmful effects manifest in their behaviour and physiology.

In using radiotelemetry to estimate duckling survival by tracking radio-marked females, certain assumptions must be met, the most important of which is that the radio

packages carried by the experimental subjects do not affect aspects of their behaviour that could influence duckling survival. Based on the results of an extensive study of recruitment in mallards, *Anas platyrhynchos*, Cowardin et al. (1985) reasoned that no conclusive statement could be made about the effects of the technique on their duckling survival estimates and, lacking decisive evidence, assumed there was no major impact. Researchers using radiotelemetry for the same purpose (to quantify duckling survival) have stressed the same assumption, and thereby justified the results obtained from what is a very convenient, yet not fully understood, technique (Ball et al. 1975, Ringelman and Longcore 1982, Talent et al. 1983, Duncan 1986, Orthmeyer 1987). However, Greenwood and Sargeant (1973: 3) warned that "such an assumption could lead to erroneous interpretations of data if unrecognized, subtle changes occur in the physiology, behavior, or well-being of the birds." Those studying brood survival must be confident that the current methods used (i.e., fitting a hen with a radio backpack before or during the nesting period) do not bias the results. Thus, it is essential that the following question be investigated thoroughly. Is the pre- and post-hatch behaviour of females altered by the presence of a radio transmitter, and if so, is the survivability of either the embryos or the ducklings influenced?

Studies of the incubation rhythms of anatids have revealed that incubating females take recesses daily, and that the eggs are subject to cooling when this occurs (Caldwell and Cornwell 1975, Derrikson 1977, Afton 1978 and 1980, Ringelman and Longcore 1982, Brown and Fredrickson 1987). A temperature decline of 10°C for up to 2 h has been recorded under natural conditions. However, when eggs are exposed to ambient temperatures for prolonged periods, the well-being of the embryo is at risk, including (1) death of the embryo (e.g. Baldwin and Kendeigh 1932), (2) sublethal teratogenic effects that affect survival only later (e.g. Thompson et al. 1976), and (3) a slowing of development (e.g. Boersma 1982, Evans 1990). Although the eggs of some birds are tolerant to chilling during development, the tolerance is lower, and decreases

as incubation proceeds, in species such as mallards (see review by Webb 1987). The percentage of mallard embryos hatching after exposure to cold, at different stages of incubation, decreases as the age of the embryo increases (Prince et al. 1969, Batt and Cornwell 1972). Therefore, if radio-marked ducks are absent from their nests for abnormally long periods, considerable cooling of the eggs may ensue, causing irrevocable damage to the embryos.

Behaviour exhibited by brood rearing ducks, especially the degree of alertness and attentiveness to the brood, may differ among individuals within a species. These differences are likely to be very important variables influencing duckling survival (Reed 1970). Although precocial, very young ducklings are not fully homeothermic until at least 2 weeks of age (Untergasser 1971). They require brooding from the hen, especially at night and and under adverse weather conditions (Koskimies and Lahti 1964, Kear 1970, Mendenhall 1979, Ringelman and Longcore 1982). If brooding is inadequate, the young may succumb to the elements (Seymour 1982). As an example, Talent et al. (1983) observed two radio-equipped mallard females leaving their broods and feeding daily in grain fields when the ducklings were less than 3 days old, even during inclement weather. Both broods disappeared within a week after hatching (apparently dead of exposure), suggesting that normal brooding behaviour may have been altered as a result of the radio packages that the females carried.

The purpose of this study was to determine if the reproductive success of female mallards is affected by the use of radiotelemetry. I hoped to understand what effects, if any, this technique has on the behaviour and physiology of the hen, and how these variables may in turn influence nesting success and duckling survival. The specific objectives were to:

(1) determine the incubation rhythms of hen mallards after radio-marking for comparison with similar behaviour in a control group.

(2) measure the extent of egg cooling in experimental and control groups

and its influence on hatchability,

(3) document survival in broods from experimental and control parents, and for ducklings from cooled and uncooled (control) eggs, and

(4) record the brood rearing behaviour of hens with and without radio backpacks.

STUDY AREA AND METHODS

The study was conducted during the summers of 1987 and 1988 near Brooks, Alberta (50°35' N, 111°54' W). Incubation, egg cooling, and hatchability data were collected from wild, radio-marked and non-radioed mallards nesting on man-made islands in the surrounding irrigation reservoirs and impoundments managed for waterfowl production by Ducks Unlimited (Canada). Captive mallards were also studied to supplement data on the above variables, and to provide information on the brood rearing behaviour of hens. The captive birds were reared from eggs taken from the wild in 1985. These birds were kept at the Brooks Pheasant Hatchery (Alberta Department of Forestry, Lands and Wildlife), allowed to pair naturally, and to breed in individual pens (8.1 m^2). Each enclosure provided partial visual isolation from other pens, contained a 4 m^2 cement pond, a nest box with straw, a supply of crushed oyster shell, and one gravity flow self-feeder containing commercial waterfowl breeder ration *ad libitum*.

Capture and radio-marking procedure

Searches for laying and incubating wild mallards took place during the first 2 weeks of May. A coloured survey flag, placed 10 m away, was used to mark the location of nests found, and the eggs present were candled (Weller 1956) to determine stage of incubation. I waited until the estimated 22nd day of incubation to trap and equip the females with radio transmitters because anatids are less likely to desert their nest, following a temporary disturbance, in late incubation than earlier (Dwernychuk and Boag

1972). Hens were captured on the nest using a manually triggered bow-net trap (Salyer 1962) and immediately moved a distance of 30 m to minimize the association of capture trauma with the nest site. All hens captured were weighed and approximately one half of the individuals (predetermined before capture) were fitted with a 22 g (2.5% of female body weight) dummy radio transmitter, after the backpack design described by Dwyer (1972). The dummy transmitters were constructed of 18 mm diameter maple dowling, drilled and weighted with lead shot, with PVC tubing for the harness. The unit was encased in a covering of dental acrylic and the harness tubing was reinforced with steel fishing line. The total elapsed time for the entire handling procedure never exceeded 12 minutes and, upon completion, the females were released and observed for any abnormal flight behaviour. Although not fitted with a radio, all control females were handled for the same amount of time. These same procedures were applied to captive mallards, with the exception that the hens were captured easily within the nest box.

Egg temperatures and incubation constancy

Following their release, egg cooling and incubation constancy were monitored for both wild and captive hens. Rustrak Z55J strip chart temperature recorders were set up immediately, to measure the extent of egg cooling for the initial period of absence after handling and during subsequent recesses. A 2.5 mm diameter thermister was affixed to the outside of one egg using two 40 mm strips of white surgical tape. The thermister was positioned about half way along the long axis of the egg so that the tape would not interfere with the hatching process at the air cell end of the egg surface. The hens accepted the arrangement without any apparent concern. An egg at the periphery of the clutch was chosen for thermister attachment because a peripheral egg is likely to cool the most during parental absence (Huggins 1941, Caldwell and Cornwell 1975). The thermister leads were drawn out through the nest bottom and hidden in vegetation up to the recorder, 5 m distant. Afterward, the clutch was covered with nest down to avoid excess egg cooling and, in the wild, exposure to avian predation.

Time-lapse 8-mm movie cameras (see Temple 1972) were used to document post-procedure absences from the nest, and subsequent nest attentiveness (incubation bouts and recesses) after the hen returned. The camera unit was usually placed 1.5-2 m from the nest bowl and camouflaged with the surrounding vegetation. A single frame was exposed every 3 or 6 min to provide a sampled documentation of nest attentiveness and recesses per day. After placing the equipment at the wild nests, an attempt was made to rearrange the surrounding vegetation to its previous undisturbed state.

Egg cooling and hatchability

In 1987 the amount of egg cooling differed greatly for wild and captive mallards; shorter absences led to minimal cooling in captivity. Therefore, in 1988 I removed eggs from captive clutches and subjected them to cooling regimes that mimicked conditions in the nests of wild radio-marked mallards. Four fertile eggs were removed from each nest (n=36 nests) on the 22nd day of incubation and replaced by four dummy eggs. Upon their removal, experimental eggs were marked with a permanent ink pen and placed into small (20 cm diameter) aluminum pans containing ample quantities of insulating down. Each of the four eggs removed from every nest was assigned to one of the following cooling regimes (temperature-duration): 20°-6h, 20°-12h, 15°-6h, and 15°-12h. Eggs were grouped by cooling temperature in the pans and placed inside coolers at either 20°C or 15°C. The number of eggs per pan depended upon the number of eggs requiring treatment on a given day (i.e., day 22 of incubation), but never exceeded eight. Following exposure to cooling, the eggs were returned to their respective nests for the remainder of incubation. A short time after the projected hatch date, all wild and captive nests were revisited to determine the number of eggs hatched. Any unhatched eggs were candled to ascertain whether or not they were infertile. Additional hatchability data were acquired from another sample of eggs (n=270) designated for another study (see Chapter III). This sample included eggs treated in the

above manner, plus cooling regimes of 20°-9h, 15°-9h, 10°-6h, 10°-9h, and 10°-12h. Since these particular eggs were incubated artificially, they were analyzed separately for hatchability because the noise of an incubator can reduce inter-egg communication, which potentially can have an effect on rate of development (Vince 1969).

Survival of captive ducklings

After hatching, ducklings were web-tagged using standard 8-mm, serially numbered monel fish tags (Natl. Band and Tag, Newport, KY). A count of brood members was taken each day for the first 2 weeks, and on every other day following, to record duckling survival. Only those ducklings that died from apparently "natural" causes were included in the analysis . This excluded all those that died as the result of (1) injuries inflicted by ground squirrels and weasels, (2) escape from their own pen, and (3) being caught in the reinforced fencing. The majority (85%) of captive brood hens used in the survival analysis hatched ducklings from experimentally cooled eggs in addition to the remainder of the clutch, which was unmanipulated. As well as being classified as cooled or not, ducklings were categorized as either light or heavy, depending upon whether they were below or above the overall mean hatch weight for all clutches.

Brood rearing behaviour

Captive mallards were allowed to hatch their clutches and the brood rearing behaviour of both radio-marked (n=18) and unmarked (n=18) hens was observed. Before ducklings left the nest, a small shelter and feeder trough (containing commercial duckling crumbles) were placed in each pen. Time budget information was obtained from hens with broods during the first 2 weeks of duckling life. Because the period most critical to duckling survival is during the first week post-hatch (Keith 1961, Reed 1970, Bengston 1972, Dzubin and Gollop 1972, Ball et al. 1975, Ringelman and Longcore 1982, Talent et al. 1983), the majority of my observations were made during this early stage. Observation bouts included all hours of the day, and were classified into the following time intervals: 0400-0800= early morning (EM), 0800-1200= late morning

(LM), 1200-1800= afternoon (AF), 1800-2200= evening (EV), and 2200-0400= night (NI). Most observations were conducted during the EM and EV periods, because I found that it was during these times that one was most likely to record the widest array of behaviours, including brooding by the hen. Observation bouts usually lasted for 2 h and concentrated on either 1 or 2 hens; focal animal sampling and instantaneous scan sampling were used (see Altmann 1974). During an observation bout, behaviours were recorded at 30-sec intervals, timed by a metronome (Weins et al. 1970). Observers used 10x50 binoculars and watched from portable blinds placed on low platforms situated outside the pens. Night time observations were aided by the use of a night vision scope (Smith and Wesson, Star-tron MK-303A) mounted on a tripod. No family was observed every day during the 2-week period, but I attempted to obtain a minimum of 10 h of observation data for each female.

During observation bouts I recorded weather conditions and the following hen behaviours: *initiate brooding* (while standing, plumage erect, wings dropped and vibrating with a "shivering action" of her flight muscles); *brood* (standing or crouching over ducklings, wings dropped, plumage may or may not be erect); *alert* (head up, neck outstretched, watchful); *comfort movements* (preen or bathe); *on water* (swim or loaf on pond); *walk* (either lead or follow ducklings around pen); *feed* (eat at feeder or "bill" the ground for vegetation, insects, grit, etc); *vocalize* (communication with ducklings- including alarm, attraction, and broody calls (Collias and Collias 1956)). The remaining behaviours occurred infrequently or were of lesser importance and, thus, were classified as *other*, they included: *stand* (on 1 or 2 legs, head and neck not in alert position); *rest* (sit or stand, bill tucked under scapular tract); *sleep* (in any posture, eyes closed). It should be noted that many of these behaviours are not mutually exclusive and could occur simultaneously. For example, a hen may preen while brooding her ducklings, she may be alert while on the water, and she may vocalize while exhibiting any number of behaviours. For this reason, the total time budget for each hen, although expressed

here as a percentage of time in each behavioural category, is greater than 100%. This, however, poses no problem for comparing between groups on a behavioural category basis. Weather information was obtained from the Atmospheric Environment Service, Environment Canada, at the Alberta Special Crops and Horticulture Research Station, 4 km from the location of this study.

Statistical analyses

The relationship between radio-marking and frequency of nest abandonment by wild hens was examined using a Fisher's exact test, status (abandon - return) and treatment (radio-marked - unmarked) were tested. A one-way ANOVA was used to test the mean body weights of returning and abandoning hens. Incubation variables (time to return, recesses/day, recess duration, bout duration) were examined with a one-way ANOVA; nest attentiveness was tested using a *G*-test of independence for percentages (Sokal and Rohlf 1981, p. 765). Mean egg cooling during absences was examined using a one-way ANOVA or, where variances were not homogeneous, with an unpaired *t*-test for heterogeneous variances.

Egg hatchability of successful nests was examined with a *G*-test for the relationship of treatment (radio-marked - unmarked) and state (hatched - unhatched). The hatchability of eggs cooled experimentally was set up as a 3x3 contingency table of state, temperature and duration, and analyzed using a log-linear model. It was decided *a priori* to test for differences in duckling survival between (1) radio-marked and unmarked hens, (2) those from cooled and uncooled eggs, and (3) those with a heavy or light hatch weight. A *G*-test of independence was used to compare state (survived - dead) with treatment.

Variables (hen age, duckling age, ambient temperature) obtained from behavioural observations on captive radio-marked and unmarked brood hens, were tested using a one-way ANOVA. The overall time-activity budget for each hen was given as a percentage of time spent in each behaviour, and was calculated from the total number

of observation hours for the individual. The two groups of birds were compared for each behaviour type using a Mann-Whitney *U*-test.

All one-way ANOVAs, *t*-tests, and *G*-tests with a Williams Correction, followed the procedures outlined in Sokal and Rohlf (1981), and were accomplished using the SPSSx statistical package (SPSS Inc. 1988). Log-linear analysis was done using the BMDP statistical software (Dixon et al. 1985). The significance level was set at $P < 0.05$ for most tests. In view of the small sample size in some of the comparisons, to avoid type II error I accepted a level of significance at $P<0.10$.

RESULTS

Nest desertion

During the summers of 1987 and 1988, 36 wild mallard females were trapped at the nest on the estimated 22nd day of incubation. Of this sample, 20 were radio-marked (RAD) and 16 were unmarked controls (CON). Following trapping and handling, seven (35%) of the RAD females deserted their nests, whereas this was the case for only one (6%) of the CON group (Table II-1). None of the nests was depredated, but one of the CON birds, the nest of which was poorly concealed, failed to hatch any eggs at all. Subsequent candling of the eggs revealed that the embryos died in late incubation, probably from overheating after the incubating female was captured during a period of hot weather.

The body weight (mean±SE) in late incubation for RAD (920±11 g) and CON (890±15 g) hens was not significantly different (one-way ANOVA, $F=2.26$, $P=0.11$). The mean weight of deserting RAD hens (907±19 g) was comparable to those not deserting (920±15 g) (one-way ANOVA, $F=0.23$, $P=0.66$). The one CON bird that deserted after trapping was extremely light, weighing only 740 g.

TABLE II-1. Clutch size and nesting success of wild mallard hens trapped on the nest in late incubation (estimated day 22). The birds were either fitted with a dummy radio transmitter (radio-marked) or handled only (unmarked).

Variable	Radio-marked	Unmarked	*P*
Number captured	20	16	
Clutch size (mean+SE)	8.75±0.32	8.69±0.39	0.84[a]
Number depredated (%)	0	0	
Number deserting (%)	7/20 (35)	1/15 (6.3)[c]	0.10[b]

[a] Probability based on a one-way ANOVA.

[b] Probability based on a Fisher's exact test.

[c] Excluding one hen that did not desert, but whose eggs apparently overheated and did not hatch.

Post-handling nest attentiveness

Data from 11 RAD and 9 CON wild mallard hens were used to determine if the attachment of radio transmitters disrupted normal incubation rhythms. Subsequent to capture, RAD birds were monitored at the nest for a total of 696 h (mean=63.3 h/hen), and CON birds for 425 h (mean=47.2 h/hen). Individuals of both groups were similar in terms of numbers of recesses per day, recess duration, incubation bout duration, and overall nest attentiveness (percentage of 24 h period on the nest) (Table II-2). After the initial capture and handling, however, RAD hens exhibited a much longer period of absence from the nest than those in the CON group. One RAD hen returned to its nest only after 18.3 h had passed and, as a result, the eggs had cooled to 14.9°C. Egg cooling immediately following handling (Table II-3) was almost twice as great among RAD females as among the CON hens. However, both egg temperature changes during recesses and minimum egg temperatures recorded were very similar between the two groups of females (Table II-3).

In 1987, similar data were recorded for 16 RAD and 12 CON captive females which were monitored for a total of 646 h (mean=40.4 h/hen) and 437 h (mean=36.4 h/hen), respectively. Since the duration of initial absences and recesses were very much shorter for captive (Table II-4) than for wild females (Table II-2), perhaps a result of close proximity to the nest, it was unecessary to compare the extent of egg cooling which, in the former group, tended to be minimal.

Egg hatchability

The proportion of eggs hatched in wild mallard nests was similar among RAD and CON females (Table II-5). Of the unhatched eggs in each group, not more than one was from the same nest. The hatching success of eggs from captive nests was similarily high for both groups of females (Table II-5).

The hatching success of mallard eggs incubated artificially, and cooled experimentally, was much the same when state (hatched or unhatched), duration, and

TABLE II-2. Incubation behaviour of radio-marked (n=11) and unmarked (n=9) wild mallard hens after being trapped on the nest late in incubation.

Variable	Radio-marked (mean value)	Unmarked (mean value)	*P*
Initial absence in minutes (range)	581.1 (117-1096)	337.8 (67-729)	0.06[a]
No. of recesses/24 h (±SE)[b]	1.49±0.25	1.50±0.25	0.94[a]
Recess duration in minutes (range) (n)	105.9 (36-272) (36)	124.6 (65-408) (23)	0.26[a]
Bout duration in minutes (range) (n)	675.9 (65-1758) (47)	604.5 (225-1320) (32)	0.48[a]
Attentiveness (range)[c]	89.3 (79.5-96.0)	86.8 (75.6-91.6)	0.19[d]

[a] Probability based on a one-way ANOVA.
[b] Recesses/day for each hen = total number of recesses/ total time minus initial absence.
[c] Percentage of 24 h period on the nest.
[d] Probability based on a *G*-test of independence with a Williams correction.

TABLE II-3. Egg and ambient temperatures (°C) during absences from the nest for radio-marked (n=11) and unmarked (n=9) wild mallards in late incubation.

Variable	Radio-marked Mean±SE (range)	Unmarked	P
Initial absence			
Egg temperature change	-10.66±1.91 (-21.6-⁻2.0)	-5.44±1.81 (-13.0-2.0)	0.07[a]
Minimum egg temperature	24.01±1.91 (14.9-35.5)	28.56±2.43 (19.5-39.0)	0.22[a]
Recesses			
Egg temperature change	-7.94±0.68 (-19.6-⁻2.0)	-9.20±1.51 (-27.0-0.0)	0.45[b]
Minimum egg temperature	27.53±0.76 (17.0-36.0)	27.22±1.54 (12.0-37.0)	0.78[b]
Ambient temperature [c]	15.64±0.56	15.13±0.72	0.54[a]

[a] Probability based on a one-way ANOVA.
[b] Probability based on a *t*-test for samples with heterogeneous variances.
[c] Overall mean of the mean ambient temperature for each period a hen was off her nest.

TABLE II-4. Incubation behaviour of radio-marked (n=16) and unmarked (n=12) captive mallard hens after being trapped on the nest and handled late (day 22) in incubation.

Variable	Radio-marked (Mean value)	Unmarked (Mean value)	*P*
Initial absence in minutes (range)	134.2 (6-474)	124.9 (6-372)	0.77[a]
No. of recesses/day (±SE)[b]	1.44±0.24	1.02±0.20	0.25[a]
Recess duration in minutes (range) (n)	54.7 (7-232) (38)	57.7 (18-192) (19)	0.76[a]
Bout duration in minutes (range) (n)	604.0 (6-1586) (55)	792.8 (167-1934) (30)	0.09[a]
Attentiveness (range)[c]	94.1 (81.9-100.0)	95.9 (90.2-100.0)	0.59[d]

[a] Probability basad on a one-way ANOVA.
[b] Recesses/day for each hen = total number of recesses/ total time minus initial absence.
[c] Percentage of 24 h period on the nest.
[d] Probability based on a *G*-test of independence with a Williams correction.

TABLE II-5. Hatchability estimates for successful (hatched one or more eggs) wild and captive mallard hens, both radio-marked and unmarked.

Variable	Radio-marked	Unmarked	P^a
Wild mallards			
No. of clutches	13	14	
No. of fertile, nonparasitic eggs	111	127	
No. of eggs hatched (%)	106 (95.5)	117(92.1)	0.38
Captive mallards			
No. of clutches	36	35	
No. of fertile eggs	319	327	
No. of eggs hatched (%)	312 (97.8)	319 (97.6)	0.83

[a] Probability based on a *G*-test of independence with a Williams correction.

temperature were analyzed using a log-linear model (Table II-6). The two-way interaction of temperature x state was not significant (G=4.91, P=0.09), but accounted for much more of the variation between the nine groups than did the interaction of duration x state (G=0.49, P= 0.78). However, hatchability did not decrease proportionally with a drop in cooling temperature. The hatching success of 20°C eggs was very high (97.4%), but dropped off about equally for eggs in the 15°C (87.8%) and 10°C (89.3%) groups.

Another group of eggs from clutches of captive mallards were cooled experimentally at four temperature-duration combinations (Table II-7) before being replaced for the completion of incubation. Only 4/132 (3.0%) eggs failed to hatch, and a log-linear analysis of state, duration, and temperature revealed no statistical difference between the 4 groups (G=2.60, P=0.11). The hatching success of 20°C eggs was 98.5% and that for 15°C eggs 95.5%.

All cooled eggs, whether artificially or naturally incubated, were grouped together for a test against uncooled controls, because in neither case was hatchability significantly different by log-linear analysis. The grouping resulted in a greater combined failure rate of 24/343 (6.5%) for cooled than for 10/401 (2.4%) control eggs (G-test of independence, G=8.65, P=0.004). Although the losses were few, eggs cooled to moderate temperatures on the 22nd day of incubation had more than twice the failure rate of control eggs.

Duckling survival

Five captive females (all in adjacent pens) lost all of their ducklings within the first two weeks post-hatching. These data were not included in the survival analysis because there was evidence to suggest that many of the deaths were caused by a long-tailed weasel, *Mustela frenata*. The problem did not persist once the predator was removed. Thirty-nine RAD and 33 CON captive females fledged ducklings, but CON females fledged proportionally fewer (263/297 (88.6%)) than RAD birds (332/350 (94.9%)) (G-test of independence, G=3.93, P=0.05; Figure II-1A). The survival of 168 ducklings

TABLE II-6. Hatchability of artificially incubated mallard eggs, cooled experimentally at three temperatures and for three durations on the 22nd day of incubation.

	Duration (h)	Temperature (°C) 10	15	20	P[a]
No. of eggs hatched (%)	6	25/29(86.2)	21/24(87.5)	26/26(100)	0.70
	9	25/28(89.3)	23/26(88.5)	24/26(92.3)	
	12	25/27(92.6)	21/24(87.5)	25/25(100)	

[a] Probability based on a *G* value obtained for a log-linear model of a 3-way interaction.

TABLE II-7. Hatchability of mallard eggs from the nests of captive hens (n=36) after being cooled experimentally (on the 22nd day of incubation) for a combination of two temperatures and two durations. The eggs were returned to the nests after the procedure.

State	Duration (h)	Temperature (°C) 15	20	P[a]
No. of eggs hatched (%)	6	30/33 (90.9)	33/33 (100)	0.11
	12	34/34 (100)	31/32 (96.9)	

[a] Probability based on a *G* value obtained for a log-linear model of a 3-way interaction.

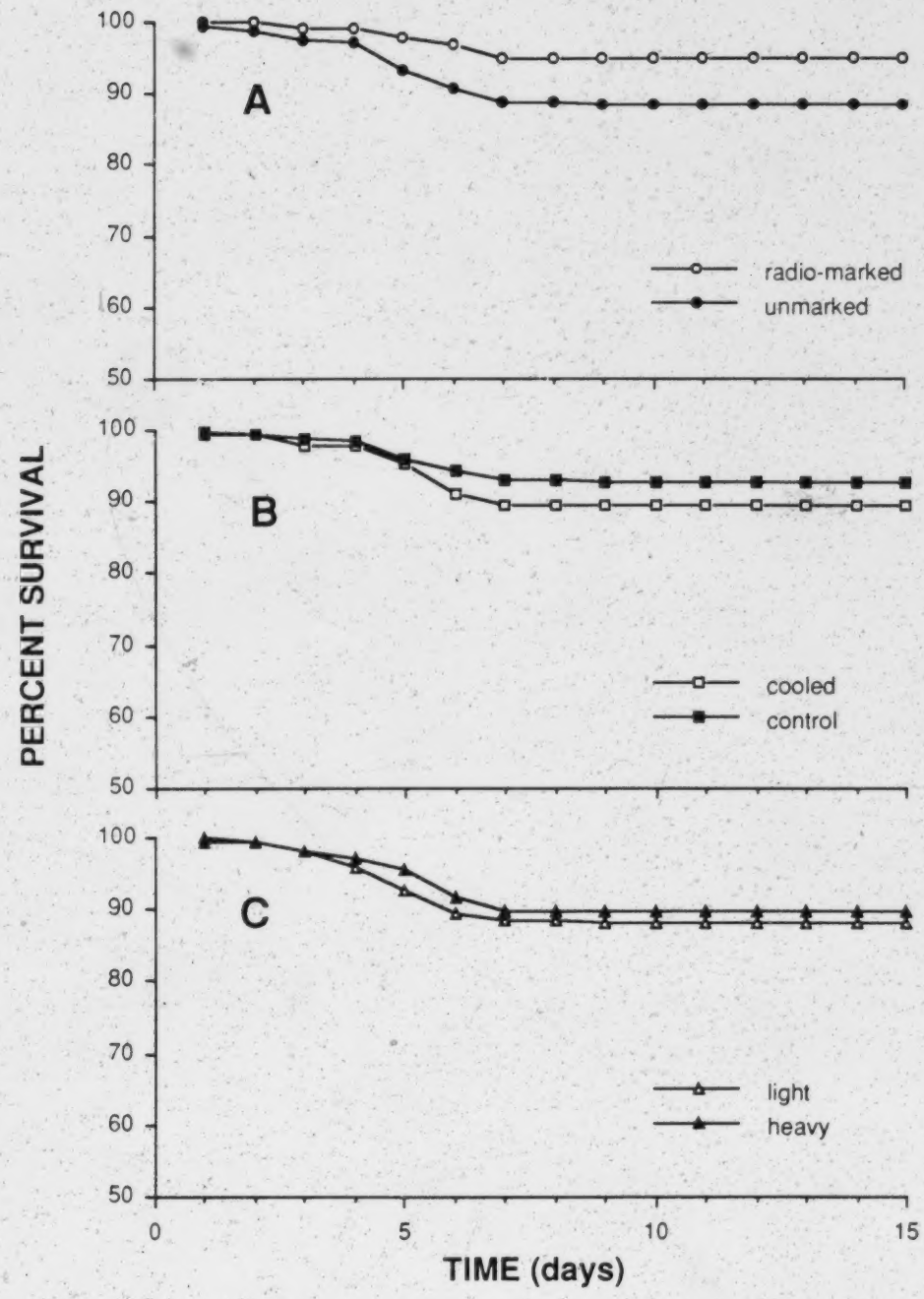

Figure II-1. Cumulative survival over time for captive mallard ducklings, either from (A) broods of radio-marked or unmarked hens, (B) cooled or uncooled eggs, or (C) for those categorized as either light (<33 g) or heavy (>33 g) at hatch.

from experimentally cooled eggs was compared with that of 400 ducklings from uncooled control eggs (Figure II-1B). The difference was small and not significant (G=1.76, P=0.27), with 10.7% dying from cooled eggs, and 7.2% from controls.

The overall mean hatch weight of the ducklings in this study was 33.02±0.23 g. Individuals above and below the mean were categorized as heavy and light, respectively. The proportion dying in either group was similar (G=0.24, P=0.58); 10.4% of the heavy and 11.9% of the light ducklings (Figure II-1C). Further subdivision of each weight category into those from cooled or uncooled eggs showed an apparent trend, but the interaction between weight and treatment was not significant (Table II-8). Nevertheless, the largest difference was between light ducklings from cooled eggs (16.0% died) and heavy ducklings from uncooled eggs (8.1% died) (G-test of indepedence, G=3.40, P=0.07). It appears that post-hatch viability is related to hatch weight and embryonic cooling. In addition, the individuals that died were not growing normally at the time, but instead were losing weight as though feeding very little (Appendix I).

Time-activity budgets of brood rearing females

Captive radio-marked (n=20) and unmarked (n=20) female mallards were observed in order to compare time-activity budgets in the first 2 weeks post-hatch. RAD hens were observed for a total of 269 h and CON hens for 261 h; the time observed (h) per hen and hen age being the same for each group (Table II-9). Both duckling age and ambient temperature can influence the brood rearing behaviour of female anatids (Mendenhall 1979, Paulus 1984, Rushforth Guinn and Batt 1985), but they too were similar for each group of hens (Table II-9). Time of day may dictate which behaviours predominate, but a breakdown of the total observation hours into proportions conducted during different intervals of the day (Table II-10) showed no differences (P>0.22) between RAD and CON birds, regardless of the time interval in question.

TABLE II-8. Number of ducklings dying during brood rearing by captive mallard hens. Ducklings were classified as either light (<33g) or heavy (>33g), and whether they were cooled experimentally as 22 day-old embryos or incubated naturally (control).

	Treatment		
Duckling size	Cooled	Uncooled	P^a
Light (%)	12/75 (16.0)	19/186 (10.2)	0.71
Heavy (%)	8/79 (10.1)	9/111 (8.1)	

[a] Probability based on a *G* value obtained for a log-linear model of a 3-way interaction.

TABLE II-9. A summary of variables obtained from behavioural observations of captive radio-marked and unmarked mallard hens during early brood rearing.

Variable	Radio-marked Mean±SE (range)	Unmarked Mean±SE (range)	P[a]
Hours observed/hen	13.43±0.80 (8.4-19.9)	13.03±0.89 (8.9-22.7)	0.75
Hen age (years)	2.40±0.15 (1-3)	2.20±0.19 (1-3)	0.64
Duckling age (days)[b]	5.68±0.49 (3-10)	5.70±0.41 (3-10)	0.91
Ambient temperature (°C)[c]	17.67±0.49 (13.6-20.4)	17.36±0.51 (13.8-20.6)	0.47

[a] Probability based on a one-way ANOVA.

[b] The overall mean of the mean duckling age for each hen, with the latter weighted by the proportion of total observation time for the group.

[c] The overall mean of the mean ambient temperature during observations on each hen, with the latter weighted by the proportion of total observation time for the group.

TABLE II-10. The percentage (mean±SE) of total observation hours conducted during each of five intervals of the day for captive radio-marked and unmarked mallard hens during early brood rearing.

Time interval (hours)	Radio-marked (n=20)	Unmarked (n=20)	P[a]
0400-0800	40.90±4.62[b]	40.95±3.77	0.49
0800-1200	9.00±3.58	9.15±2.28	0.27
1200-1800	5.65±1.91	3.25±1.55	0.22
1800-2200	30.00±3.42	27.00±4.21	0.25
2200-0400	14.45±3.63	19.65±3.72	0.30

[a] Probability based on a Mann-Whitney *U*-test.
[b] The mean of the means for all hens in the group.

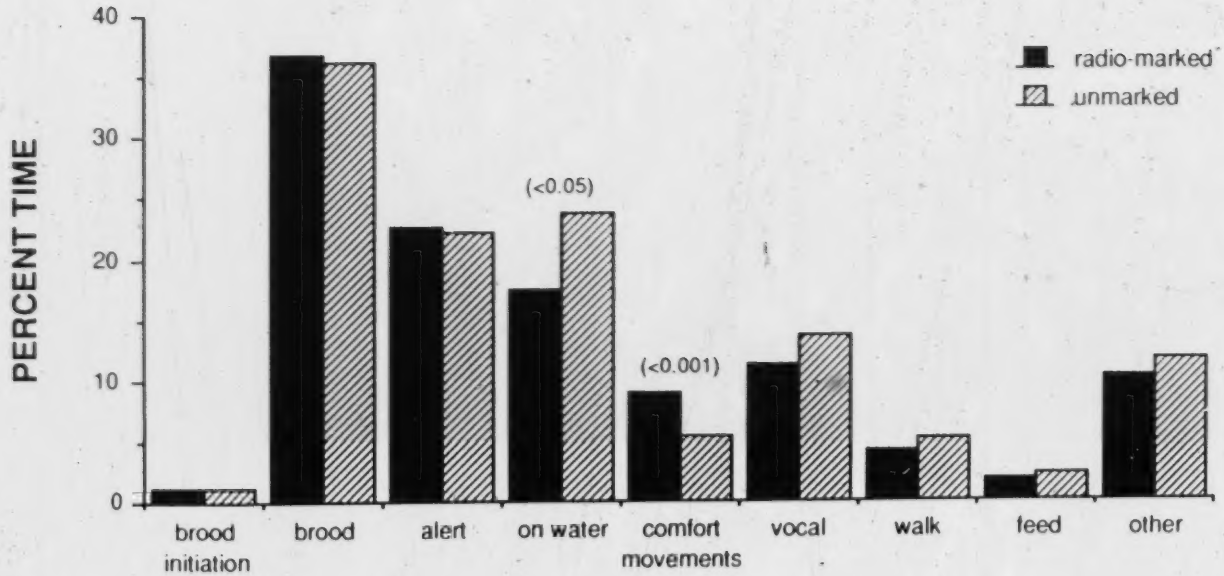

Figure II-2. Percent of time spent by brood rearing female mallards, either radio-marked (n=20) or unmarked (n=20), in various behavioural activities (significant probability values, based on Mann-Whitney *U*-tests, in parentheses).

Time-activity budgets of brood rearing hens were expressed as a proportion (% of total time observed) of time spent in each behaviour (Figure II-2). Birds in the RAD and CON groups were similar for the following activities: brood initiation (1.1 vs 1.1%), brooding (36.8 vs 36.3%), alert (22.8 vs 22.3%), walking (4.2 vs 5.2%), feeding (1.9 vs 2.1%), and being vocal (11.4 vs 13.7%). However, RAD hens spent significantly more time performing comfort movements (8.9 vs 5.4%), and less time on the water (17.5 vs 23.9%). These differences suggest that radio packages influence at least some aspects of the behaviour of mallard hens with broods.

DISCUSSION

Frequency of nest abandonment

Results of this study demonstrate clearly that fitting incubating mallard females with a radio backpack increases the probability of nest abandonment. These observations are consistent with other investigators using radio-marked mallards: Yarris (pers. comm.) reported abandonment rates of 36% and Orthmeyer (1987), 15%. Among incubating northern pintails, *Anas acuta*, and gadwalls, *Anas strepera*, 35% deserted following capture and radio-marking (Duncan, unpubl. data). Ten of 41 (24%) adult Canada geese, *Branta canadensis moffitti*, may have deserted after being fitted with radios during the hatching process (Eberhardt et al. 1989). Nest abandonment, however, appears to be infrequent when incubating anatids are only captured and banded. Frequencies of 3-10% for island nesting lesser scaup, *Aythya affinis*, and gadwall (Vermeer 1968), and 7% for island nesting mallards (Keith 1961) are similar to levels observed among control birds in this study.

It is probable that birds abandoning their nests are experiencing considerable stress, being unable to adjust sufficiently to the presence of the radio package. Observations of captive and wild ducks indicated that, following capture and radio

attachment, the birds were preoccupied with the backpack (Greenwood and Sargeant 1973, Dwyer 1972, Gilmer et al. 1974, Perry 1981, this study). Considerable time is spent preening, pulling, and biting the transmitter and harness, apparently in response to this foreign stimulus. An additional factor that can lead to nest abandonment in anatids is poor body condition (Ankney and MacInnes 1978, Gloutney 1989). This phenomenon may have been exemplified in this study by a very light, non-radioed hen that abandoned its nest following capture and handling. The relationship between body condition and nest abandonment may be more pronounced with the added stress imposed by carrying a radio package (Orthmeyer 1987). Therefore, one would predict that radio-marked birds would abandon more frequently either later in the nesting season or when they are in poor body condition. Furthermore, it cannot be implied that a bird returning to the nest following radio-fitting is fully adjusted to the presence of the marker. Instead, for such a bird, the urge to continue incubating the clutch may surpass the urge to desert and escape from the backpack.

Nest attentiveness and egg cooling

Contrary to expectations, both radio-marked and unmarked hens displayed comparable incubation constancy upon returning to the nest. Recess frequency, duration, and time of day for this study were similar to those reported for radio-marked black ducks, *Anas rubripes*, (Ringelman et al. 1982), unmarked mallards (Gloutney 1989), and white-winged scoters, *Melanitta fusca*, (Brown and Fredrickson 1987). These larger bodied species usually take one or two recesses per day, either in the early morning and evening, or just in the evening. Drent (1975) determined that recesses taken in the afternoon-evening (warmest time of the day) minimize cooling rates, and thus reduce recovery energy costs because eggs usually require more time to be heated back to normal incubation temperature than they take to cool. In addition, although the incubation rhythm of individual birds may differ significantly, mallards (Caldwell and Cornwell 1975), northern shovelers, *Anas clypeata*, (Afton 1980), black ducks (Ringelman et al. 1982),

and many other avian species (Drent 1970, 1975) respond to a drop in ambient temperature with an increased incubation constancy. Although birds were monitored for only a fraction of the incubation period, results of this study gave no indication that radio-marked mallards exhibited abnormal incubation rhythms, during either warm or cool weather (perhaps because there were no notable extremes during the period investigated).

The absence of hens after radio marking was much longer than for unmarked birds, and in one case, eggs that were left unattended for 18.3 h had cooled to 15° C. Such heat loss, which is dependent on prevailing ambient temperatures as well as duration of absence (Drent 1975, Caldwell and Cornwell 1975), can reduce reproductive success by causing lowered hatchability or slowed development; the sensitivity to such perturbations increases with age of the embryo (Hunter et al. 1976, review in Webb 1987). In fact, a causal relationship seems to exist between incubation interruption and low hatchability (Vermeer 1970, Nisbet 1975, Boersma and Wheelwright 1979). Thus, the interruption of incubation caused by the radio-marking technique, can leave the eggs susceptable to prolonged cooling which may lead ultimately to decreased viability of the embryos.

Hatchability of cooled eggs

Egg hatchability for all wild mallards in this study was consistent with findings for non-radioed anatids (Keith 1961, Vermeer 1968 and 1970, Dzubin and Gollop 1972) and radio-marked anatids (Reed 1975, Orthmeyer 1987) and galliforms (Erikstad 1979). Talent (1980), however, found that successful radio-marked mallards hatched only 78% of their eggs, and Clark et al. (1987) had an apparent hatch rate of 83%. In a study of red grouse, *Lagopus lagopus scoticus*, Lance and Watson (1977) discovered that two radio-marked hens hatched only 51% of their eggs. Although the results do not suggest reduced hatchability under the conditions prevailing during this study, low levels recorded by others have led some to conclude that trapping and radio-marking

incubating ducks may have an adverse effect on subsequent hatchability of their eggs (Talent 1980).

For avian embryos to develop properly, eggs must be maintained within a relatively narrow range of temperatures during the course of incubation. If the egg temperature frequently falls below the "physiological zero temperature" (i.e., temperature at which development stops: 25-27°C) for extended periods, it may have negative effects on embryonic development and hatchability (Haftorn 1988). Although the difference was small, hatching success of either naturally or artificially incubated eggs cooled experimentally on the 22nd day of incubation, was somewhat lower than for uncooled controls. This is consistent with the results found for older embryos of mallards (Prince et al. 1969, Batt and Cornwell 1972), and other bird species (Romanoff 1949, MacMullan and Eberhardt 1953, Moreng and Bryant 1956, Lundy 1969, Bennet et al. 1981, Gaston and Powell 1989). Avian embryos are apparently less tolerant of the effects of prolonged cooling with increasing age and severity of exposure. Since the temperatures were not extreme, however, the results of this study only hinted at a relationship between egg cooling and hatchability.

Short periods of cooling at moderate temperatures, however, appear adaptive for many avian embryos, and hatchability may even increase as a result of the stimulating effects of alternate cooling and incubation (Baldwin and Kendeigh 1932, Oppenheim and Levin 1975). Even so, most avian embryos in the later stages of development cannot survive exposure to temperatures <10°C for 24 h (Webb 1987, Haftorn 1988). For mallards, at least, there exists a wide range of temperature tolerance, as demonstrated by the eggs of two deserted nests in this study. Both clutches were unincubated for more than 48 h; during this time the 11 eggs of clutch A were cooled to a minimum of 15.5°C, and eight eggs in clutch B cooled to 5°C. Retrieval and subsequent artificial incubation of the eggs resulted in the following: clutch A - one embryo died during the period of cooling, six revived but died just before pipping, and four hatched within a

span of four days (the yolk sac of one was not enclosed fully by the abdominal wall, and it died 1 day later); clutch B - three embryos died during the cooling period, two remained alive until the pipping stage, and three hatched within a span of 1 day. Of the ducklings that hatched from each clutch, all were heavier than average, having a dry hatch weight of 34 g or more.

In summary, of those researchers reporting hatchability of eggs from radio-marked ducks, some found it to be lower for radioed females, others did not. The attachment of a radio to an incubating hen can result in prolonged exposure of the clutch to ambient temperatures; but moderate cooling temperatures appear to have only a minor influence on hatchability. Anatid eggs may have a greater tolerance to extreme temperatures than most other species (Webb 1987). Mallard embryos from large eggs appear more capable of surviving extreme cooling than those from small eggs. Perhaps larger embryos are more cold-resistant as a result of greater metabolic heat production during the period of stress (Batt and Cornwell 1972). Caution is advised, however, because the percentage of hatched birds is not a complete measure of cooling tolerance; the subsequent survival of the hatchlings must also be considered.

Duckling survival

The majority of duckling mortality in this study occurred during the first week post-hatch, apparently the most critical period for neonates in wild broods as well. These early deaths have most often been attributed to predation (Talent et al. 1983, Mendenhall and Milne 1985), starvation (Kear 1965, Duncan 1986), exposure to inclement weather (Keith 1961, Koskimies and Lahti 1964, Bengston 1972, Makepeace and Patterson 1980, Duncan 1986), and unexplained losses during overland moves (Dzubin and Gollop 1972, Ball et al. 1975). Less often overcrowding (Titman and Lowther 1975) and congenital weakness (Keith 1961) are implicated in early deaths. In this study of captive birds, losses were more likely the result of either exposure or congenital weakness, because all other factors were virtually eliminated.

Although control hens fledged slightly fewer of their ducklings than radio-marked birds, the discrepancy cannot be explained by either mean duckling size or the ratio of cooled to uncooled eggs, as both variables were similar for each group of hens. Perhaps the results would have been different had the majority of ducklings found dead not been isolated outside their own pen. Nevertheless, these survival values for captive birds do not preclude that the results obtained using this marking technique are unbiased for wild ducks. Some researchers have determined that radio-marked females are far less successful than unmarked birds at raising broods to fledging. Clark et al. (1987) found that radioed mallards had significantly smaller broods of older ducklings than unmarked hens, and concluded that radioed hens produce less young per surviving brood. Ringelman and Longcore (1982) estimated that daily brood survival was significantly lower for radio-fitted black ducks. The overall gosling survival of 49% for radio-marked Canada geese, *Branta canadensis moffitti*, (Eberhardt et al. 1989) was lower than the 61% for neck-collared Canada geese (MacInnes et al. 1974, Zicus 1981). In addition to anatids, radio-marked pheasants and grouse (Phasianidae) have experienced similar problems. Radioed hens have been documented to have a lower chick survival than unmarked birds (Erikstad 1979), as well as higher brood abandonment (Kuck et al. 1970, Carter 1974, Warner 1975, Maxon 1978). Few researchers (Clark et al. 1987, Orthmeyer 1987, Yarris pers. comm.), however, acknowledge that a radio package on the parent may lead to a reduction in offspring survival.

Duckling hatch weight and the effects of prolonged embryonic cooling appeared to influence neonatal survival; heavy ducklings from uncooled eggs survived better than light ducklings from cooled eggs. This implies that either prolonged embryonic cooling or light hatch weight, or both, placed ducklings at a disadvantage for the critical post-hatch period. Experiments have demonstrated that the survival time of neonate mallards (Vangilder 1980), snow geese, *Anser caerulescens caerulescens*, (Ankney 1980), Canada geese (Lessells 1982), red grouse (Moss et al. 1981), and willow

ptarmigan, *Lagopus lagopus*, (Steen et al. 1988), was correlated with hatch weight. Also, heavier chicks in several species within the altricial-precocial spectrum survive better to fledging than lighter chicks (Parsons 1970, Nisbet 1973, Schifferli 1973, Davis 1975, Lundberg and Väisänen 1979, O'Connor 1979, Boersma et al. 1980). Schifferli (1973) stated that a heavier hatch weight may confer two advantages on the young: (1) the chick may actually have a larger body, reflecting a relatively advanced state of development, or (2) it may possess relatively more body reserves.

Metabolic reserves of newly hatched chicks are in the form of unassimilated yolk, subcutaneous fat, and proteinaceous tissues (Kear 1965, Marcström 1966, Parsons 1970, Bancroft 1985, Peach and Thomas 1986, Duncan 1988). Heavier hatchlings have absolutely more body reserves, and it is thought that these reserves may be crucial to the early survival of precocial and semi-precocial young (Parsons 1970, Ricklefs et al. 1978, Ankney 1980, Lessells 1982, Rhymer 1982, Thomas and Peach-Brown 1988).

Older duck embryos exhibit a thermogenic response to cooler temperatures (Khaskin 1961, Freeman 1964, Rol'nik 1970). Since egg metabolism is fueled almost exclusively by lipids (Romanoff 1967, Vleck and Vleck 1987), prolonged exposure of embryos to suboptimal temperatures may deplete some of the energy reserves required for subsistence after hatch. Also, the absolute energy content increases with egg size because larger eggs contain more albumen and yolk (Meathrel and Ryder 1987). Therefore, heavier embryos may have an advantage over light ones when cooled for extended periods, which may help explain the better post-hatch survival of heavy ducklings from uncooled eggs.

In conclusion, the pattern of duckling mortality in captivity was similar to that reported for wild broods, with the majority occurring in the first week. At least a portion of the mortality in this study appeared to be the direct result of prolonged embryonic cooling, which affected the post-hatch survival of smaller neonates more

severely. Caution must be used when attempting to extrapolate these results to radio-marked mallards in the wild. Captive birds were not subject to several selective pressures (predation, foraging costs, inter and intraspecific interactions) that are faced daily by wild hens and their broods. Without intensive field obervations, it is difficult to determine the impact that the radio-marking technique has on subsequent duckling survival. However, the evidence presented in this study, and others, suggest that it is no longer valid to assume that fitting the female parent with a radio backpack does not have an adverse effect on the survival of her ducklings.

Time-activity budgets

The brood rearing behaviour of radio-marked mallards in this study differed from controls in that they preened more, and spent less time on the water. Researchers testing for long-term behavioural changes in radio-fitted anatids (Greenwood and Sargeant 1973, Gilmer et al. 1974, Perry 1981) and galliforms (Boag 1972) have obtained similar results for preening, feeding, and time on water (anatids only). At least some bird species are unable to adapt to the irritation of a radio backpack, as demonstrated by high preening rates that remained elevated for some time (Gilmer et al. 1974, this study). A backpack (accompanied by a neck and body loop) on a duck may also result in water running along the harness tubing and wetting the down and skin beneath the waterproof contour feathers (Boag pers. comm.). This may help explain their apparent aversion to water. To exacerbate this problem, the feathers beneath the transmitter itself are often worn and presumably less water repellent.

Although captive birds in this study were able to meet their metabolic demands by spending little time feeding, reduced feeding by radio-marked birds can apparently lead to considerable weight loss (Schladweiler 1969, Greenwood and Sargeant 1973, Perry 1981). Additional weight loss can add to the stress on females, especially if they are already experiencing the high physiological demands imposed by nesting and brood rearing (Krapu 1981, Gatti 1983, Hohman 1986). The consequence for wild hens may

be high duckling mortality, especially if they reach a point where, in order to survive, they must sacrifice vigilance for more intensive feeding (Gatti 1983). This stress can also manifest itself through reduced vocal communication and attentiveness to the ducklings. It has been shown that communication is important in (1) monitoring the positions of brood members and (2) providing warning to potential dangers, because isolated ducklings are at a greater risk to permanent separation, predation and brood mixing (Collias and Collias 1956, Titman and Lowther 1975).

In addition to self-maintenance activities and vigilance, brood hens must provide their ducklings with additional heat, select the rearing wetland, and may even direct them to the best foraging patches (Ringelman and Longcore 1982). In the field, however, it is impossible to assess fully the impact of radio transmitters on brood survival without directly observing for changes in these behaviours. Contrary to what most believe, it appears that radio-marked individuals fail to adjust completely to the presence of the backpack. Since ducks in captivity are absolved of many of the stresses encountered in the wild, it can be argued that any differences in behaviour, manifested in the pens, would be compounded in the field. Likewise, lack of evidence in captivity cannot necessarily be extrapolated to mean no effect in the field (Boag 1972). Results presented here confirm the findings of other investigators; the behaviour of a bird is altered unconditionally with the attachment of a radio backpack. In light of these findings, forcing an incubating duck to carry a radio backpack raises serious implications for the subsequent survival of the ducklings.

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III. NEONATE BODY RESERVES: THE INFLUENCE OF EGG COOLING AND BODY SIZE.

INTRODUCTION

The lipid content of eggs of precocial species is large relative to that of altricial species. The energy available for embryonic and immediate post-embryonic development increases directly with lipid content (Ricklefs 1979, Sotherland and Rahn 1987). It is thought that the greater the reserves the more advantageous it is for newly hatched, self-feeding precocial young which may require several days to attain efficient foraging skills (Kear 1965, Marcstrom 1966, Ricklefs et al. 1978). Precocial young are believed to sustain themselves in the immediate post-hatch period by assimilating the contents of the yolk sac and body fat deposits (Kear 1965, Marcstrom 1966, Duncan 1988). Yolk is used for catabolic and synthetic purposes (Marcstrom 1966, Bancroft 1985, Peach and Thomas 1986, Duncan 1988), and a larger yolk volume may confer a selective survival advantage post-hatching, as suggested for the young of shags, *Phalacrocorax aristotelis*, (Coulson et al. 1969), herring gulls, *Larus argentatus*, (Parsons 1970) and mallards, *Anas platyrhynchos*, (Birkhead 1985). Larger anatid hatchlings with correspondingly larger lipid reserves survive starvation considerably longer than smaller ones (Krapu 1979, Ankney 1980, Thomas and Peach Brown 1986). Larger mallard hatchlings also have a relatively greater tolerance of cold stress because of a better capacity to produce heat and a smaller surface to volume ratio (Rhymer 1982). Thus, yolk and body lipid reserves are generally considered to be an important food and energy source for newly hatched birds, those individuals with relatively more of these reserves may have a selective advantage, particularly under certain environmental conditions.

The adverse effects of egg cooling, manifested by slightly decreased hatchability and survival (especially for smaller ducklings, see Chapter II Results), may be associated

with a depletion of crucial body reserves. Researchers have long known that embryos of precocial species increase their metabolic rate to facilitate heat production (Romanoff 1941, Romijn aand Lokhorst 1960, Khaskin 1961, White and Kinney 1974, Caldwell and Cornwell 1975, Vleck et al. 1980, Whittow 1986). This phenomenon is evident after 10 days of incubation, increasingly so thereafter for the domestic duck (Khaskin 1961) and the herring gull, *Larus argentatus* (Drent 1970). Older duck embryos exhibit a thermogenic response to cooler temperatures (Khaskin 1961, Rol'nik 1970), effectively retarding egg cooling during periods of parental absence (Webb 1987). Embryo metabolism is fueled almost exclusively by lipids (Romanoff 1967, Drent 1970, Whittow 1986, Sotherland and Rahn 1987); at least 42% of the fresh egg lipids are consumed during the incubation period by domestic chicks (Romijn and Lokhorst 1960) and domestic ducks (Khaskin 1961).

There may be a relationship between hatchling body reserves and prolonged embryonic cooling. Shawer and Moreng (1975) noted that cold-stressed embryos of domestic fowl weighed less than non-stressed individuals. Boersma and Wheelwright (1979) suspected that chick mortality in fork-tailed storm petrels, *Oceanodroma furcata*, was linked to depleted yolk reserves, and may have accounted for the smaller size of neonates neglected longer as embryos. Since absolute energy content increases with egg size (Meathrel and Ryder 1987), heavier embryos may have an advantage over light ones when cooled for extended periods. This may explain, at least in part, the better post-hatch survival of heavy ducklings from uncooled eggs than light ducklings from cooled eggs (see Chapter II).

The purpose of this study was to determine if prolonged egg cooling, such as that caused by radio-marking an incubating hen, influenced in any way the body reserves or subsequent growth of neonate mallards. I also examined the relationship between duckling size and the amount of body reserves available for the critical period immediately following hatch. The specific objectives were to

(1) determine, by comparison with a control group, if the body reserves of neonate mallards were depleted by prolonged cooling as 22-day-old embryos,

(2) evaluate the relationship between body composition and duckling hatch weight, and

(3) measure growth rates of ducklings from cooled or uncooled eggs, and of those hatching with either a light or heavy body weight.

STUDY AREA AND METHODS

The study was conducted during the summer of 1988 using ducklings hatched by captive birds, and from clutches of eggs collected from the wild near Brooks, Alberta (50°35' N, 111°54' W). The latter were transferred to a commercial incubator at the Brooks Pheasant Hatchery (Alberta Department of Forestry, Lands and Wildlife) where they were held at 37.5°C and 88% relative humidity. On the 22nd day of incubation a sample of 90 eggs was subjected to experimental cooling. Each egg was assigned randomly to one of nine cooling regimes, generated by three temperatures (20, 15, and 10°C) and three durations (6, 9, and 12h) (see Chapter II: Methods). After treatment the eggs were returned to the incubator where they were held until they hatched. Ducklings, when dry and fluffy (12 h-old), were weighed to the nearest 1.0 g and the sex determined by cloacal examination. Each individual was then sacrificed using a lethal dose of chloroform, placed in a labelled plastic bag, and frozen for subsequent laboratory analysis.

Duckling body reserves

At the laboratory, the liver and yolk sac (including contents) were excised from each duckling and the components (liver, yolk sac, carcass) were weighed to the nearest 0.01 g. The components were then oven-dried to a constant weight at 70°C. The water

content (*WATER*) of each component was the difference between the weight of the dry residue (*DWT*) and the wet weight (*WWT*). The dried carcasses were broken apart and homogenized with a small coffee grinder (Braun Aromatic KSM 2); livers and yolk sacs were ground to a powder using a mortar and pestle. Lipids were extracted from the dry residue using petroleum ether in a Soxlet apparatus (Dobush et al. 1985). The dried livers and yolk sacs were small enough to extract the total lipids in one run, whereas two replicates (approximately 2 g each) were required for each carcass. Lipid content (*LIPID*) was the difference in mass of the dried sample before and after extraction; the remaining residue was referred to as lean dry weight (*LDW*). Other variables calculated after the extraction procedure were *WI* (water index = $WATER \times LDW^{-1}$) and *LI* (lipid index = $LIPID \times LDW^{-1}$).

Duckling growth

Ducklings from experimentally cooled and normally incubated eggs were hatched by captive mallard hens (see Chapter III Methods), and weighed periodically until they fledged. They were weighed to the nearest 1 g using a Pesola spring scale every other day from 0-8 days, every third day from 8-14 days, and every fourth day from 14-54 days-old (approximate age at fledging). Ducklings were fed *ad libitum* commercial starter crumbles (22% protein) for the first 2 weeks, grower crumbles (18% protein) for the next 4 weeks, and a mainterance ration (16% protein) for the remaining period.

As a measure of growth rate for each duckling, I selected the slope (*b*) of a straight line fitted by linear regression procedures to the weights taken at intervals between 6 and 42 days of age. Within this period the growth curve was not statistically different from linear. In addition, the absolute growth rate (g/day) was computed for each interval in the growth curve. For each duckling I was able to determine the maximum absolute growth rate (*MAXAB*) and the age (*AMAXAB*) at which it occurred.

Statistical analyses

The variables obtained from the lipid extractions were used to ascertain if there was a relationship between egg cooling, size, or sex, and neonate body reserves. For each body component, analysis of variance was used to test for the effects of temperature, duration, body size and sex, and the interaction of temperature and duration (Sokal and Rohlf 1981). Each body component was also examined for differences between ducklings from cooled and uncooled eggs using one-way ANOVAs. I tested the allometric relationship in each component by regression of the logarithm of component weight on the logarithm of duckling body weight (Ricklefs et al. 1978). This procedure yielded a value for the slope (b) according to the relationship $Y=aX^b$. Values of b were tested with a t-test and those not significantly different from 1.0 indicated that component weight increased in direct proportion to body weight. Slopes >1.0 or <1.0 indicated a proportionately greater or lesser increase, respectively, in component weight relative to body weight.

Duckling growth variables were examined using a one-way ANOVA for the effects of treatment (cooled or uncooled) and hatch weight. The sexes were kept separate in all comparisons because the growth curves of males and females differ slightly (Rhymer 1982). Analysis of variance and log-log regressions were conducted using the SPSSx statistical package (SPSS Inc. 1988), with a significance level of 0.05. All logarithmic transformation of data was to the base 10.

RESULTS

Influence of egg cooling on neonate body reserves

Liver. The mean wet weight of livers for mallard ducklings from uncooled eggs was 1.29 g, comprising 4% of total body weight. The mean water fraction was 69% (WI=5.00), while lipids accounted for 53.8% of the dry weight (LI=1.17). The liver

composition of 86 ducklings from cooled eggs was examined and the values plotted on a figure to demonstrate whether temperature or duration was more influencial in determining the outcome (i.e., 6 h duration included eggs cooled at 20, 15, and 10°C). The values for both *LIPID* and *LI* decreased as cooling duration increased (Figure III-1), but only for *LIPID* was this trend statistically significant (Table III-1). Ducklings from eggs that endured the most extreme cooling (15°C-12 h and 10°C-12 h) were pooled for a comparison with those from uncooled eggs. Although liver size was similar between the two groups, ducklings from uncooled eggs hatched with a higher *LI* and lower *LDW* (Table III-2). The size and sex of ducklings were examined for absolute differences in liver composition. Sex type did not influence ($P \geq 0.21$) any of the variables analyzed, but the same did not hold true for duckling size. The livers of heavy ducklings (n=36) were significantly larger than for light ducklings (n=50), and had greater values for *LDW* (0.22 vs 0.19 g) and *WATER* (1.03 vs 0.84 g) (Table III-1). Although light ducklings possessed a higher *LI* (1.05 vs 0.95), it was probably an artifact produced by a lower *LDW* (used in the *LI* calculation), because the liver *LIPID* content was similar for both groups (P=0.15, one-way ANOVA).

Yolk sac. For ducklings from uncooled eggs, the size of the yolk sac averaged 2.19 g (6.8% of body weight), but varied considerably, ranging from 0.80-6.20 g. The wet weight contents were 49% water (*WI*=2.21), and of the dry weight 56% was lipids (*LI*=1.27). Using experimentally cooled eggs, I tested all composition variables with analysis of variance for the effects of cooling temperature, duration, and the interaction of both, but found no statistically significant differences (Table III-1). However, the *WWT*, *LDW*, *WATER*, and *LIPID* content decreased rather consistently with cooling temperature and duration (Figure III-2). A comparison of ducklings from eggs cooled at the two extremes with uncooled controls revealed that yolk sac size was 25% larger for control ducklings, but the high degree of variability within this group may have masked a significant difference between the two means (Table III-2). There were no differences in

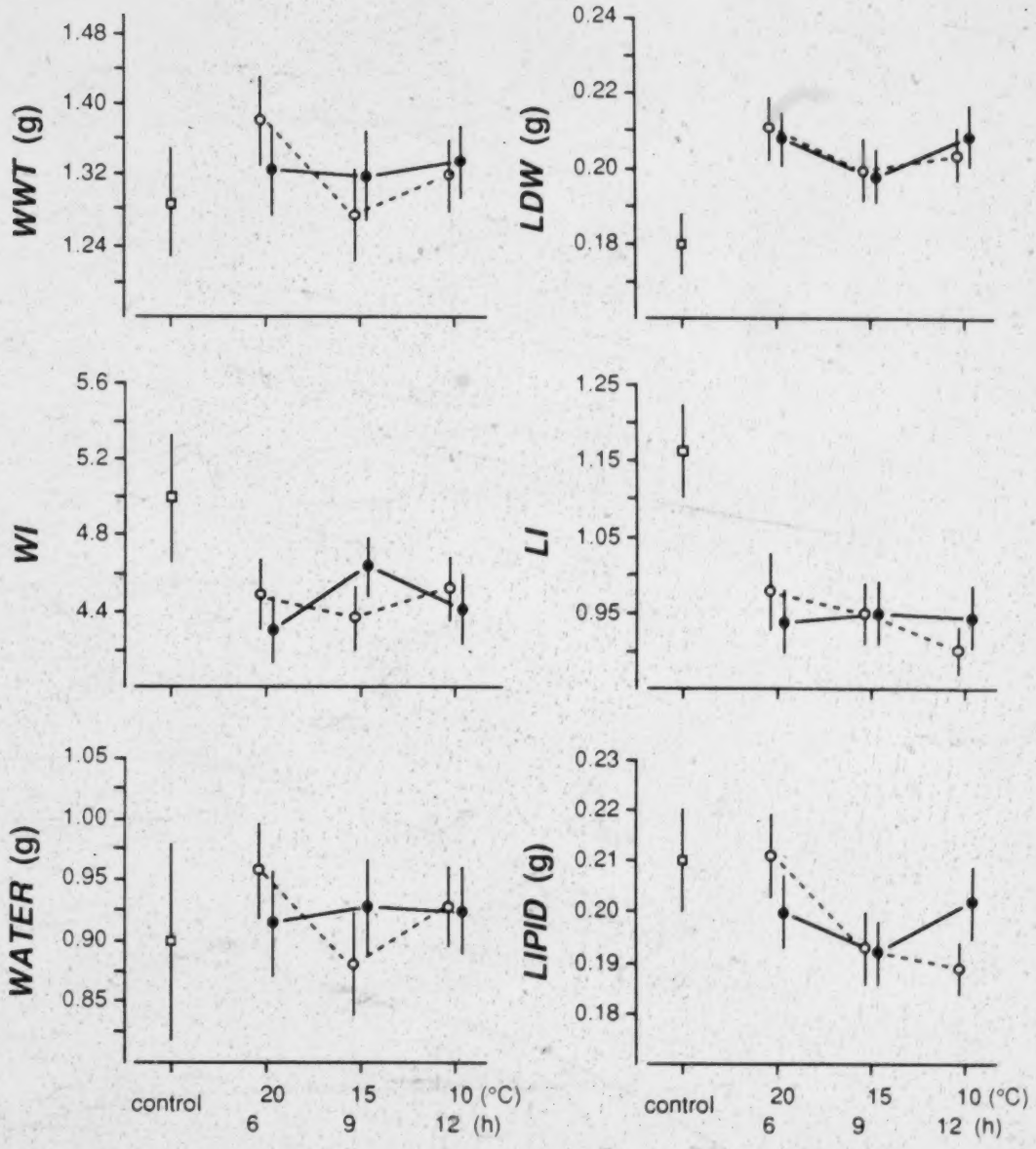

Figure III-1. Content variables for the livers of mallard ducklings hatched from eggs either cooled on the 22nd day of incubation or not (control). The means and standard error bars are given for controls (□) and those grouped by cooling temperature (●) and cooling duration (○).

Table III-1. Summary of analyses for the composition of four mallard duckling components (liver, yolk sac, carcass, whole duckling) in relation to egg cooling, size, and sex. The values in the body of the table are probabilities obtained by one-way and two-way analyses of variance. (continued on next page)

	Composition Variables						
Variable	*WWT*	*DWT*	*WI*	*LI*	*LDW*	*LIPID*	*WATER*
LIVER							
Temperature	0.96	0.40	0.36	0.97	0.53	0.60	0.96
Duration	0.24	0.11	0.79	0.37	0.54	0.05	0.36
Size	0.00	0.00	0.14	0.04	0.00	0.15	0.00
Sex	0.52	0.21	0.39	0.88	0.30	0.34	0.71
Temperature x Duration	0.11	0.38	0.17	0.46	0.24	0.67	0.09
YOLK SAC							
Temperature	0.79	0.91	0.52	0.64	0.82	0.95	0.62
Duration	0.29	0.35	0.49	0.74	0.50	0.28	0.24
Size	0.00	0.00	0.01	0.08	0.00	0.00	0.00
Sex	0.28	0.22	0.21	0.76	0.36	0.15	0.40
Temperature x Duration	0.68	0.64	0.61	0.57	0.42	0.86	0.55

Table III-1. (continued)

Variable	*WWT*	*DWT*	*WI*	*LI*	*LDW*	*LIPID*	*WATER*
CARCASS							
Temperature	0.64	0.58	0.30	0.12	0.96	0.18	0.48
Duration	0.63	0.93	0.51	0.72	0.74	0.92	0.50
Size	0.00	0.00	0.01	0.14	0.00	0.00	0.00
Sex	0.50	0.52	0.66	0.62	0.76	0.52	0.54
Temperature x Duration	0.57	0.62	0.55	0.71	0.37	0.77	0.63
WHOLE DUCKLING							
Temperature	0.64	0.91	0.55	0.20	0.97	0.53	0.58
Duration	0.99	0.56	0.44	0.54	0.88	0.35	0.93
Size	0.00	0.00	0.41	0.01	0.00	0.00	0.00
Sex	0.16	0.07	0.39	0.23	0.13	0.08	0.37
Temperature x Duration	0.84	0.92	0.83	0.45	0.99	0.59	0.81

Note: *WWT*, wet weight; *DWT*, dry weight; *WI*, water index; *LI*, lipid index; *LDW*, lean dry weight; *LIPID*, total lipid; *WATER*, total water.

Table III-2. Body component variables for 12-hour-old mallard ducklings that were either cooled experimentally (15°-12h and 10°-12h) on the 22nd day of incubation, or not (control). (continued on next page)

Variable	Control (Mean±SE)	Experimental (Mean±SE)	P
Liver	(n=22)	(n=20)	
Wet weight	1.29±0.06	1.31±0.05	0.80[a]
Dry weight	0.39±0.02	0.40±0.01	0.73[a]
Water index	5.00±0.23	4.49±0.16	0.07[a]
Lipid index	1.17±0.04	0.95±0.04	<0.001[a]
Lean dry weight	0.18±0.005	0.21±0.009	0.01[b]
Lipids	0.21±0.01	0.19±0.01	0.31[b]
Water	0.90±0.06	0.91±0.04	0.84[a]
Yolk sac	(n=22)	(n=20)	
Wet weight	2.19±0.33	1.64±0.15	0.14[b]
Dry weight	1.11±0.18	0.81±0.09	0.15[b]
Water index	2.90±0.23	2.91±0.25	0.88[a]
Lipid index	1.27±0.14	1.66±0.17	0.09[a]
Lean dry weight	0.49±0.11	0.34±0.05	0.23[b]
Lipids	0.62±0.10	0.47±0.05	0.20[b]
Water	1.08±0.14	0.82±0.07	0.10[b]
Carcass	(n=20)	(n=17)	
Wet weight	28.71±0.59	29.35±0.63	0.46[a]
Dry weight	8.62±0.21	8.48±0.21	0.69[a]
Water index	3.40±0.08	3.51±0.04	0.24[b]
Lipid index	0.46±0.02	0.43±0.02	0.27[a]
Lean dry weight	5.92±0.13	5.96±0.13	0.80[a]
Lipid	2.70±0.12	2.53±0.12	0.33[a]
Water	20.09±0.56	20.89±0.44	0.28[a]

Table III-2. (continued)

Variable	Control (Mean±SE)	Experimental (Mean±SE)	P
Total body	(n=20)	(n=16)	
Wet weight	32.19±0.78	32.23±0.78	0.94[a]
Dry weight	10.12±0.24	9.53±0.23	0.09[a]
Water index	3.35±0.14	3.50±0.04	0.29[b]
Lipid index	0.54±0.02	0.48±0.02	0.03[a]
Lean dry weight	6.59±0.15	6.44±0.16	0.46[a]
Lipids	3.53±0.13	3.09±0.12	0.02[a]
Water	22.07±0.67	22.49±0.55	0.68[a]

[a] Probability based on a *t*-test.
[b] Probability based on a *t*-test for heterogeneous variances.

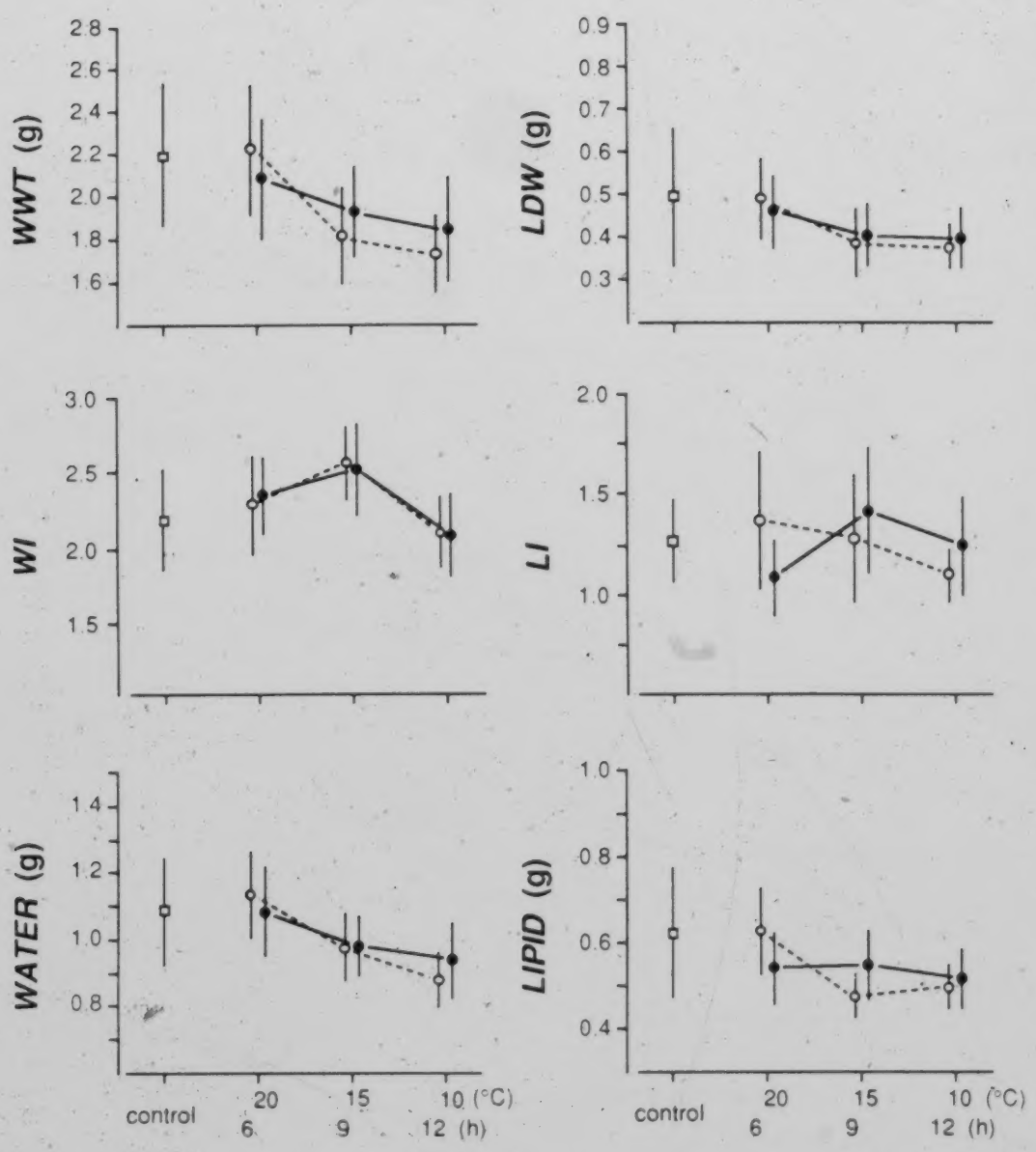

Figure III-2. Content variables for the yolk sacs of mallard ducklings hatched from eggs either cooled on the 22nd day of incubation or not (control). The means and standard error bars are given for controls (□) and those grouped by cooling temperature (●) and cooling duration (○).

yolk composition between the sexes, but body size at hatch was a very important factor (Table III-1). Heavy ducklings (n=36) hatched with absolutely larger yolk sacs than light ducklings (n=50), and had significantly higher values for *WWT* (2.92 vs 1.37 g), *LDW* (0.69 vs 0.25 g), *LIPID* (0.80 vs 0.37 g), and *WATER* (1.37 vs 0.74 g).

Carcass. The carcass of mallard ducklings in the control group contained conspicuous fat deposits, especially in the leg area, comprising 31.3% (*LI*=0.46) of the dry weight at hatch. Carcass fats accounted for 77% of the total lipid reserves of the neonate. The carcass also contained 70% water (*WI*=3.40). The composition of 73 duckling carcasses, from experimentally cooled eggs, was examined for the effects of temperature and duration, and the variables were found to be similar for the two groups (Table III-1). There was an apparent relationship, however, between water content and cooling duration; both *WI* and *WATER* increased as duration increased (Figure III-3). Carcass composition of the 15°C-12 h and 10°C-12 h groups combined was not different from that of control ducklings (Table III-2). There was no difference between the sexes ($P>0.50$), but substantial differences were encountered for the two size catagories (Table III-1). Large ducklings had greater values for *LDW* (6.24 vs 5.73 g), *LIPID* (2.75 vs 2.33 g), and *WATER* (22.17 vs 19.75 g). Therefore, heavy ducklings had not only larger yolk sacs, but also a larger carcass mass, in absolute terms.

Whole duckling. The average hatch weight of mallard ducklings in the control group was 32.2 g. Water comprised 68.6% (*FWI*=3.35) of the wet weight and lipids 34.9% (*LI*=0.54) of the dry weight. None of the composition variables tested was significantly affected by cooling temperature or duration during incubation (Table III-1). Water and lipid content, however, appeared to be influenced by the severity of egg cooling. *WI* increased with both lower temperature and longer duration, whereas *LI* and *LIPID* had a tendency to decrease as duration increased (Figure III-4). Ducklings from eggs cooled at 15°C-12 h and 10°C-12 h had a lower *LI* and possessed lower overall lipid levelsthan controls (Table III-2). A comparison of the two size categories revealed

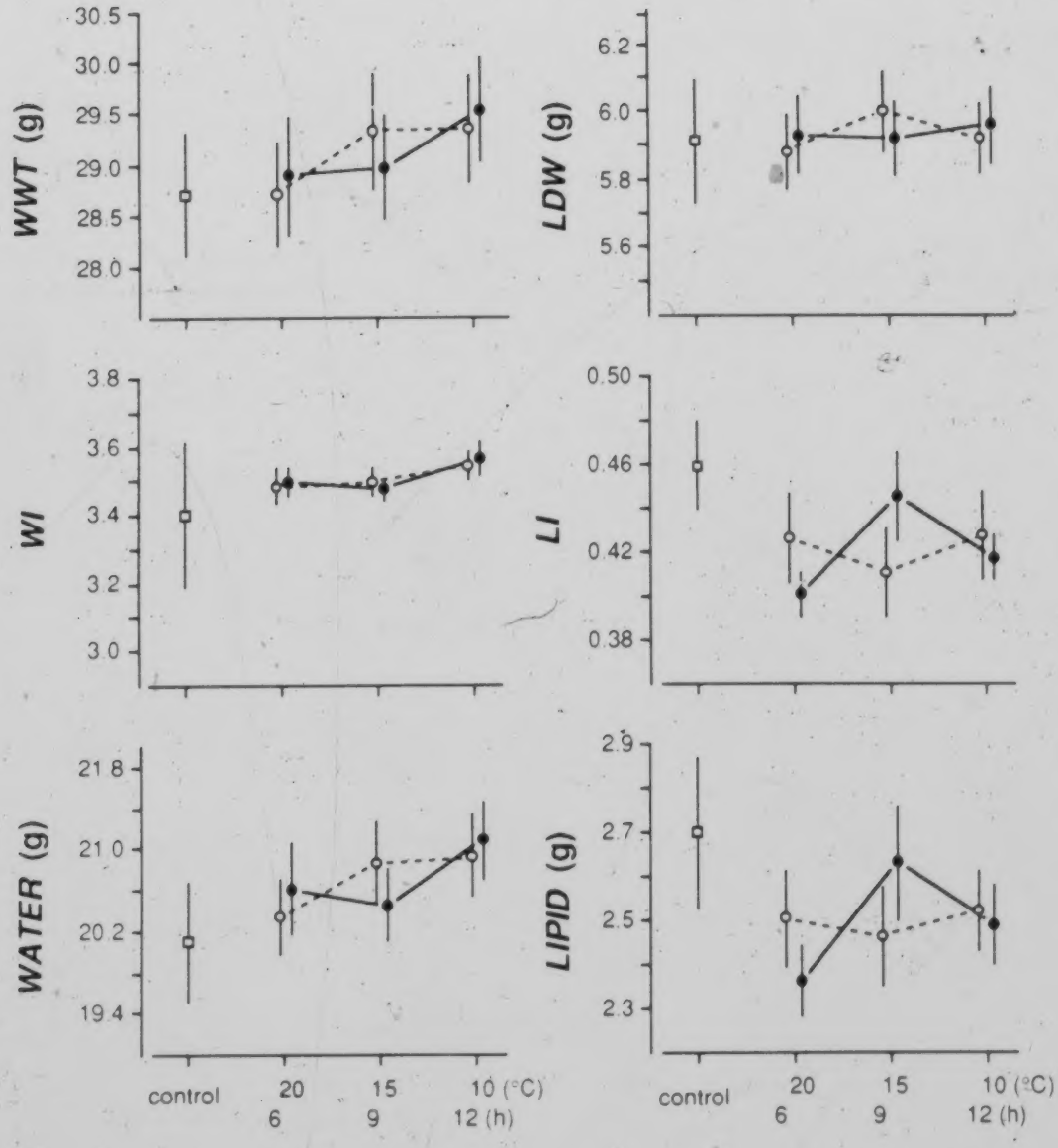

Figure III-3. Content variables for the carcasses (lacking liver and yolk sac) of mallard ducklings hatched from eggs either cooled on the 22nd day of incubation or not (control). Means and standard error bars are given for controls (□) and those grouped by cooling temperature (●) and cooling duration (○).

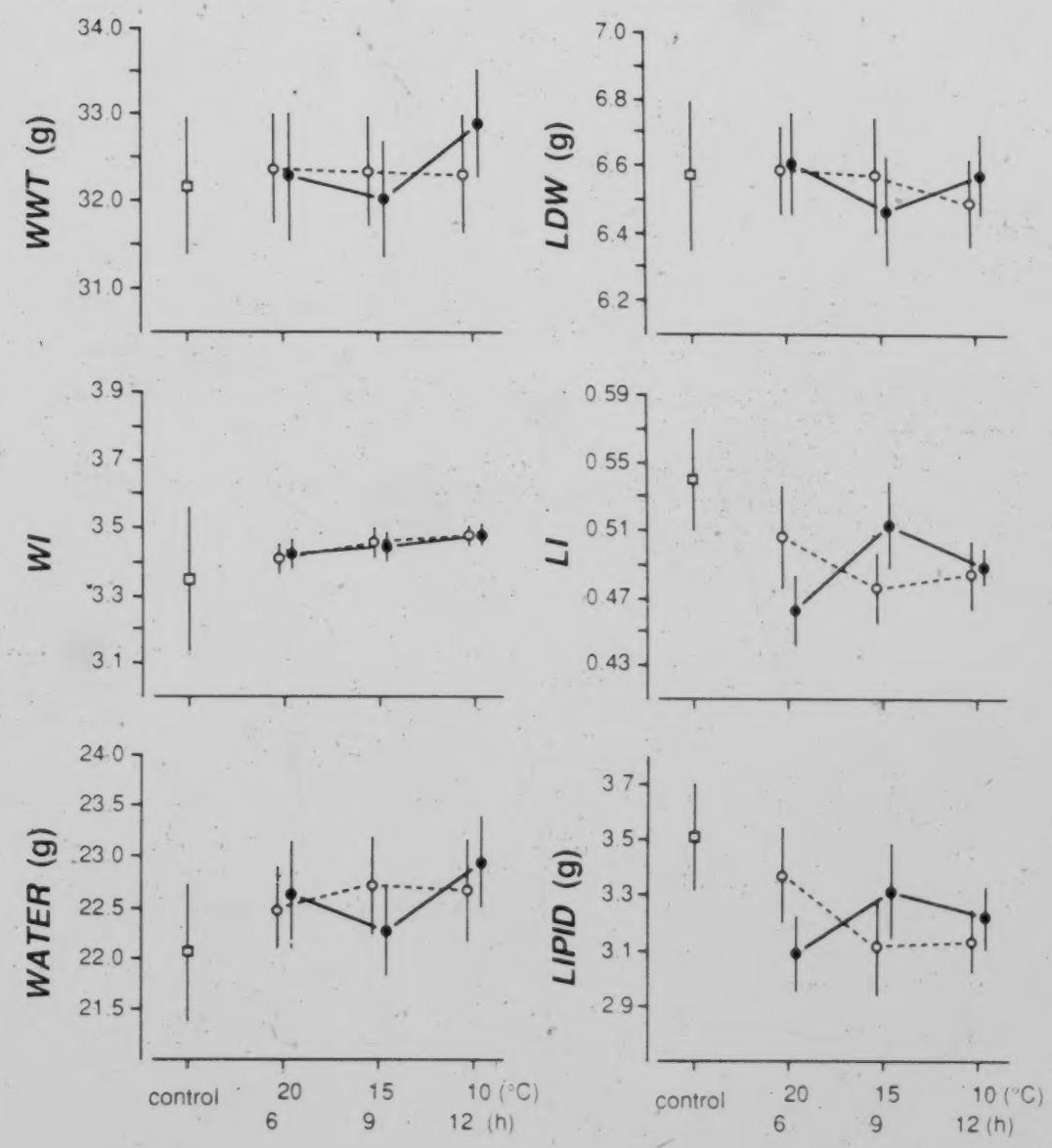

Figure III-4. Content variables of whole mallard ducklings hatched from eggs either cooled on the 22nd day of incubation or not (control). Means and standard error bars are given for controls (□) and those grouped by cooling temperature (●) and cooling duration (○).

that heavy ducklings (n=28) had greater values than light ones (n=44) for *LDW* (7.11 vs 6.18 g), *LI* (0.53 vs 0.46), *LIPID* (3.72 vs 2.89 g), and *WATER* (24.67 vs 21.30 g)(Table III-1). In absolute terms, therefore, larger mallard ducklings hatch with greater lipid, protein, and water reserves.

Relationship between body components and neonate mass

Log-log regression analyses indicated that the body reserves of mallard ducklings generally increased in proportion (b=1.0) to body size, but this relationship did not hold for all components (Table III-3). All measures of body composition for the duckling as a whole increased in direct proportion to body size, including *LIPID* and *WATER*. For the carcass on the other hand, only *LIPID* followed an allometric relationship, all others had a $b<1.0$. One may expect the results for carcass composition to be the same as those for the whole duckling (b=1.0). This apparent discrepency can be explained by the fact that the yolk sac increased proportionately more than did body size. All log-log regressions of yolk sac composition on body weight were statistically significant ($P<0.001$), indicating that $b \neq 1.0$ (Table I.I-3). In fact, b was much greater than 1.0 for all variables tested, demonstrating that heavier ducklings had proportionately more yolk reserves. Liver size and water content increased in direct proportion to body size, but the lipid fraction did not (Table III-3).

Neonate growth

The mean weight of captive mallard ducklings, hatched without any prolonged egg cooling, was 32.94 g (Table III-4). They usually lost weight for the first 2 days post-hatch, and again after the 7th week as they neared fledging. The maximum absolute growth rate (*MAXAB*) achieved was between ca. 37.0 g/day (females) and 38.5 g/day (males), attained at 23.2 and 24.4 days, respectively. Both males and females exhibited similar patterns of growth, although males fledged at heavier weights in both control and experimental groups (Table III-4). The 4 groups of ducklings from cooled eggs did not differ ($P>0.09$) from one another for any of the growth variables, and were therefore

Table III-3. Summary of log-log regression analyses of components (Y) on duckling body weight (X) for neonate mallards.

Component	r^2	b (95% CI)[a]	P[b]
Liver (n=96)			
WWT	0.31	1.06 (0.74-1.38)	>0.60
DWT	0.12	0.56 (0.25-0.87)	<0.01
LDW	0.16	0.78 (0.41-1.15)	>0.20
LIPID	0.03	0.34 (-0.05-0.72)	<0.001
WATER	0.31	1.28 (0.88-1.67)	>0.10
Yolk sac (n=96)			
WWT	0.40	3.99 (2.99-4.99)	<0.001
DWT	0.35	4.23 (3.04-5.42)	<0.001
LDW	0.38	5.44 (4.03-6.86)	<0.001
LIPID	0.27	3.49 (2.32-4.66)	<0.001
WATER	0.42	3.76 (2.85-4.67)	<0.001
Carcass (n=81)			
WWT	0.80	0.79 (0.70-0.88)	<0.001
DWT	0.43	0.66 (0.49-0.83)	<0.001
LDW	0.44	0.60 (0.45-0.75)	<0.001
LIPID	0.18	0.79 (0.41-1.18)	>0.20
WATER	0.79	0.84 (0.74-0.94)	<0.01
Whole duckling (n=80)			
DWT	0.76	0.99 (0.87-1.12)	>0.90
LDW	0.71	0.88 (0.75-1.00)	>0.05
LIPID	0.38	1.19 (0.85-1.53)	>0.20
WATER	0.93	0.99 (0.93-1.04)	>0.50

[a] Slope of regression and 95% confidence interval.
[b] Probability based on a t-test for b=1.0.

Table III-4. Growth variables (mean±SE) of male and female mallard ducklings from uncooled eggs (control) and those from eggs cooled on the 22nd day of incubation.

Growth variables	Sex	Treatment		P^a
		Control (n=119)	Cooled (n=102)	
Hatch weight (g)	M	32.97±0.43 (n=63)	33.54±0.45 (n=54)	0.36
	F	32.91±0.47 (n=56)	32.65±0.51 (n=48)	0.70
Slope (b)[b]	M	27.94±0.44	26.89±0.57	0.14
	F	25.81±0.38	24.33±0.51	0.02
MAXAB (g/day)[c]	M	38.48±0.72	37.76±0.84	0.52
	F	36.89±0.96	34.64±0.64	0.06
AMAXAB (days)[d]	M	24.41±0.93	24.15±0.80	0.83
	F	23.21±0.78	25.50±1.10	0.09
Final weight (g)[e]	M	1123.25±11.82	1093.80±15.80	0.13
	F	983.77±11.95	966.98±13.80	0.36

[a] Probability based on a one-way ANOVA.
[b] Slope obtained by linear regression techniques for the growth phase between 6 and 42 days.
[c] Maximum absolute growth.
[d] Age at maximum absolute growth.
[e] Weight at fledging (54 days-old).

combined for a comparison with those from uncooled eggs (Table III-4). Ducklings from cooled eggs grew at a slower rate (*b*), the difference being significant for females, but fledging weight was comparable to that of their cohorts from uncooled eggs (Table III-4).

Growth of females was apparently influenced by both egg cooling temperature (control, 20°C, 15°C) and duration (control, 6h, 12h). The overall growth rate decreased with increasing duration (control=25.8, 6h=25.1, 12h=23.5, P=0.02, one-way ANOVA), but the pattern was less consistent for temperature (control=25.8, 20°C=24.1, 15°C=24.5, P=0.06, one-way ANOVA). In addition, *MAXAB* showed a consistent decline with both decreasing temperature (P =0.10) and increasing duration (P=0.11). Growth parameters for male ducklings were far less influenced by egg cooling temperature or duration (P>0.19, one-way ANOVA). Size at hatching also influenced the individuals rate of growth. Every growth parameter tested showed a statistical difference between ducklings classed as either light or heavy at hatching (Table III-5).

DISCUSSION

Influence of egg cooling on neonate body reserves

The livers of newly hatched precocial birds have a high fat content (Entenmann et al. 1940, Marcstrom 1966, Duncan 1988). These stores increase many-fold through the incubation period, especially during the later stages (Noble and Moore 1964). This mobilization of lipids from the yolk to the liver is striking in mallards, especially in the last 2-3 days before hatching (Kear 1965). The livers of mallard ducklings in this study had a high lipid content, but the proportion of lipid decreased as egg cooling duration increased. It is possible that the cooling treatment either (1) interfered in some way with the process of lipid transfer to the liver, or (2) caused more lipid to be used for embryonic metabolism. The liver in ducklings is the site of considerable thermogenesis

Table III-5. Growth variables (mean±SE) of male and female mallard ducklings catagorized as either light (<33 g) or heavy (>33 g) at hatching.

Growth variables	Sex	Hatch weight		P[a]
		Light (n=115)	Heavy (n=106)	
Hatch weight (g)	M	30.55±0.27 (n=60)	35.61±0.27 (n=57)	0.00
	F	30.22±0.30 (n=55)	35.67±0.25 (n=49)	0.00
Slope (*b*)[b]	M	26.50±0.54	28.48±0.41	0.01
	F	24.19±0.46	26.15±0.39	0.00
MAXAB (g/day)[c]	M	37.20±0.81	39.15±0.71	0.08
	F	34.24±0.70	37.66±0.95	0.00
AMAXAB (days)[d]	M	25.60±0.84	22.91±0.88	0.03
	F	25.20±1.01	23.22±0.83	0.14
Final weight (g)[e]	M	1089.75±15.47	1130.61±11.05	0.05
	F	954.02±10.84	1000.71±14.15	0.01

[a] Probability based on a one-way ANOVA.
[b] Slope obtained by linear regression techniques for the growth phase between 6 and 42 days.
[c] Maximum absolute growth.
[d] Age at maximum absolute growth.
[e] Weight at fledging (54 days-old).

(Steen and Gabrielsen 1986), as well as the synthesis and storage of glycogen. The glycogen made available late in incubation may be necessary for successful hatching (Webb 1987) and the proper functioning of the central nervous system (Freeman and Vince 1974). Research has shown that the cooling of chicken embryos (Delphia et al. 1967) and day-old chicks (Davison and Lickiss 1979) results in a depletion of hepatic glycogen. Further research is required to understand the relationship between hepatic lipid and glycogen, and their role in embryo and neonate development.

The yolk sacs of mallard ducklings from uncooled eggs in this study accounted for 6.8% of the body weight, similar to that of 12-hour-old mallards (5.4%)(Kear 1965) and northern pintails, *Anas acuta*, (6.6%)(Duncan 1988). So too, the lipid content of the yolk sac (56% of the dry weight) was similar to 51% for other mallards (Ricklefs 1977) and 56% for northern pintails (Duncan 1988).

Yolk sac size had a tendency to decrease with increasing severity of exposure to egg cooling, suggesting that a relationship exists between prolonged embryonic cooling and yolk reserves at hatching. Boersma and Wheelwright (1979) reported a similar relationship in fork-tailed storm petrel chicks (those hatching from eggs neglected for the longest period had the smallest yolk sacs at hatching), and suggested that yolk reserves were diverted to maintenance while the eggs were unattended. Embryos of precocial species use their yolk reserves for maintenance, especially later in incubation (Vleck et al. 1980, Drent 1975, Whittow 1986), and of the the portion used, the majority (88%) is lipid (Romanoff 1967, Sotherland and Rahn 1987). During the hatching process itself there is a dramatic decrease in visible yolk material, much of it catabolized to accommodate the increased energy expenditure at this time (Kear 1965, Peach and Thomas 1986). Thus, the results of this study support the findings of Boersma and Wheelwright (1979) that prolonged egg cooling during incubation leads to a reduction in yolk reserves of the neonates that hatch. Although exposures were much less severe in this study, the trend was still apparent.

Newly hatched anatids generally use the remaining yolk material within 5 days of hatching (Kear 1965, Marcström 1966, Peach and Thomas 1986, Duncan 1988). Materials resorbed from the yolk sac during this early period are used in catabolic processes, for synthetic purposes, and for storage in the body. Remnant yolk may also be important for the development of homeothermy in newly hatched birds (Ar and Yom-Tov 1978). It contributes synthetic material for hepatic glycogen (Rinaudo et al. 1982), which in turn may be involved in the maintenance of body temperature (Freeman 1965). Removal of the yolk sac caused a reduction in metabolic rate for neonate chickens (Barott et al. 1936), and significantly increased the cooling rate for black-legged kittiwake , *Rissa tridactyla*, hatchlings (Klaassen et al. 1987), demonstrating its importance as a nutrient reserve for catabolism. Yolk does not function solely as a source of energy, but also provides materials for growth, even for starved hatchlings (Kear 1965, Peach and Thomas 1986, Duncan 1988). Thus, any reduction in the yolk reserves remaining at hatch, as demonstrated here, has potential survival implications for the ducklings.

Carcass composition of mallard ducklings appeared to be less affected by the egg cooling treatments. Carcass lipids comprised 31% of the dry weight, and accounted for 77% of the total lipid reserves at hatch. Similar lipid levels (34.5%) in mallard ducklings have been documented (Marcström 1966). However, Duncan (1988) found that lipids comprised 40% of the carcass composition for northern pintails, although as a portion of the total reserve it remained comparable (72%).

The results from this study demonstrate that neonate mallards have a high overall fat content ($L/=0.54$), slightly more than the value ($L/=0.45$) obtained by Rhymer (1982), but within the range (0.43-0.54) for other anatids (Sugden and Harris 1972, Peach and Thomas 1986, Hepp et al. 1987). Water content was also quite similar to that cited in other studies (66-68%). On the other hand, Duncan (1988) reported that 12-hour-old northern pintails were relatively higher in both lipid ($L/=0.60$) and water (78%) content. It

is difficult to interpret the findings for pintails, and the reason for the difference from other ducklings. Perhaps it is a reflection of the higher demands for over-land movements among neonate pintails (Krapu 1974, but see Duncan 1987).

The total lipid levels in ducklings from uncooled eggs was higher than for those from cooled eggs, and decreased with increased severity of cooling (especially duration) in the latter. The fat combusted during embryonic development is an expression of energy expenditure, and the majority is used near the end of incubation (Drent 1970, Vleck et al. 1980) and lost as metabolic heat (review in Webb 1987). Prolonged incubation, that caused by parental absences for example, increases the energy costs of development and maintenance, thus adding to the metabolic demands on the embryo (Boersma and Wheelwright 1979, Whittow 1986). Frequent or extended exposure of eggs to below-optimal incubation temperatures, can cause thermal stress in the embryos and lead to below normal hatch weights in chickens (Shawer and Moreng 1975) and fork-tailed storm petrels (Boersma and Wheelwright 1979). Although the rate of lipid metabolism probably varies among individual embryos (Alisauskas 1986, Hepp et al. 1987), it is undoubtedly the most important energy source for development and thermogenesis. Experimental cooling of mallard eggs in this study apparently caused an increase in the amount of lipid reserves catabolized during development. Further, this depletion (albiet small) of crucial energy stores may be responsible, in part, for the trend towards lower survival rate of ducklings from cooled eggs (see Chapter II).

Relative water content in ducklings from cooled eggs was higher than that for controls, and increased as the treatment became more severe (longer duration). Although not statistically significant, this very small difference may be important to the individual. Ricklefs (1979) stated that the water content in body tissues is an index of developmental maturity, and decreases with increasing maturity at hatch for the range of species studied. Perhaps extended periods of prolonged embryonic cooling cause the neonate's tissues to be less developed at hatching, compared to those incubated

normally. An alternative to this hypothesis is that high water content is a reflection of the increased metabolic demands imposed upon the embryo by thermal stress. Dry matter is metabolized during incubation, and the cumulative water content is increased further by metabolic water production (Ar and Rahn 1980). Ar and Rahn (1980) also discovered that the mass of lipids consumed is almost identical to the amount of water produced. This reciprocal relationship was apparent for mallards in this study (see Figure III-4), if indeed some of the metabolic water produced still remained in the tissues at hatching.

In conclusion, the high lipid content of eggs of precocial species seems to be selected for in that it provides reserves to be used for (1) embryonic development, (2) energy expenditure during the hatching process, and (3) early post-hatch maintenance and growth. Prolonged egg cooling during incubation, such as that caused by extended periods of parental absence, can lead to a lower lipid index in the liver, reduce the yolk reserves, and cause an overall depletion of important energy reserves. The changes in neonate body reserves appear to be correlated with the severity of egg cooling (especially the duration), and may cause a direct increase in the energy expended for embryonic thermogenesis and prolong the incubation and hatching process. Such a reduction of crucial body reserves may ultimately lower the chances for duckling survival in the first few days after hatch (see Chapter II).

Relationship of body components to neonate mass

The results of this study demonstrate that larger mallard ducklings hatch with absolutely more lipid, protein, and water than smaller ducklings. This corroborates the findings for other precocial (Ankney 1980, Thomas and Peach Brown 1988) and semi-precocial species (Parsons 1970, Alisauskas 1986). In addition, the relative levels of total body reserves in neonate mallards are highly correlated with body size; lipid, protein, and water content increased in direct proportion (b=1.0) to hatchling weight. Similar results were documented for the total lipid in day-old mallards (Rhymer 1982)

and newly hatched wood ducks (Hepp et al. 1987), but the same relationship apparently did not exist (b=0.72) for Canada goose goslings (Thomas and Peach Brown 1988). Indirect support for the results herein is also given by evidence obtained from freshly laid eggs of blue-winged teal, *Anas discors*, (Rohwer 1986) and Japanese quail, *Coturnix coturnix japonica*, (Ricklefs et al. 1978). In each case, lipid levels increased at least in direct proportion to egg size. Further, for the precocial species studied in detail it has been demonstrated that egg quality and composition are linked closely to hatchling quality (Parsons 1970, Ricklefs et al. 1978, Ankney 1980), and that larger neonates have a survival advantage because they contain larger lipid reserves (Ankney 1980).

The proportional, or allometric, relationship eluded to above was not apparent for all body components in the analysis. Liver size varied in direct proportion to body size but lipid content was essentially constant between weight classes. In addition, carcass (lacking liver and yolk sac) wet weight was highly correlated (r^2=0.80) with body weight, but the slope of the relationship was slightly less than 1.0. Only the lipid fraction of the carcass increased in direct proportion to body weight, yet this relationship showed a high degree of variability. Contrary to the results for livers and carcasses, however, the fraction of lipid, water, and lean dry weight in the yolk sacs of neonate mallards increased relatively more rapidly than did body weight. Thus, larger ducklings hatched with relatively larger yolk sacs, containing proportionately more reserves, than smaller ducklings. These results differ greatly from those for the small sample of day-old mallards studied by Rhymer (1982), in which the yolk sac component decreased as body weight increased. In both data sets, however, there is a good deal of variability in yolk sac size, much more than exists for hatch weight itself. Given this variation in the amount of yolk remaining at hatch, what then are the consequences for the ducklings in the period following hatch?

If the systematic relationship between body reserves and body size of neonate mallards has any value, it must derive primarily from some advantage after hatch. It it is

generally accepted that a larger body size and/or larger lipid reserves translate into a survival advantage for that individual (Parsons 1970, Schifferli 1973, Ricklefs et al. 1978, Birkhead 1985). First, neonates with more reserves can sustain themselves for longer periods of food shortage (Krapu 1979, Ankney 1980), partly because higher body fat levels may reduce catabolism of the carcass tissues when fasting occurs (Thomas and Peach Brown 1988). Second, the ability of neonates to maintain homeothermy is influenced by body size and lipid reserves. Although during cold stress birds maintain body temperature primarily by shivering thermogenesis in the lean tissues (Dawson and Hudson 1970), the yolk sac itself may be important as a source of energy rich compounds and nutrients essential for the development of homeothermy (Ar and Yom-Tov 1978). Thus, an enhanced resistance to body temperature fluctuations and an increased capacity to produce heat increases the survivability of heavier ducklings at low ambient temperatures (Rhymer 1982). Finally, because the yolk sac also provides essential nutrients for early growth, a larger yolk sac may translate into an early growth advantage. In some studies, the greater reserves of larger eggs accelerated the growth rate of the young that subsequently hatched (Schifferli 1973, Rhymer 1982, Järvinen and Ylimaunu 1984, but see Thomas and Peach Brown 1988), and for young mallards the higher lipid levels in heavier ducklings caused them to have proportionately more lipid reserves at fledging (Rhymer 1982).

In summary, overall lipid levels increased at least in direct proportion to the body size of day-old mallards, but of all the variables measured, lipid content showed the highest degree of variability. The size and composition of the yolk sac increased relatively more rapidly than body weight, and ranged greatly in size at hatching. A larger body size and corresponding larger lipid reserves may confer a survival advantage during periods of food shortage and cold stress. The benefits of having more body reserves at hatch may also have a lasting effect throughout the growth period, and beyond. Although the ultimate success of young mallards in the wild is influenced by a number of

genetic and environmental factors, such a favourable relationship between body reserves and size would appear to enhance the survival of larger neonates.

Neonate growth rates

The overall pattern and rate of growth for mallard ducklings in this study is comparable to that reported elsewhere (Sugden et al. 1981, Rhymer 1982). However, ducklings of both sexes hatching from eggs subjected to cooling, grew at a slower rate and fledged at slightly lighter weights, than ducklings from uncooled eggs. This phenomenon was more apparent in females than males, both the overall growth rate and maximum absolute growth decreased with increased cooling duration. A similar reduction in growth rate was reported by Romanoff (1935, 1936) for domestic turkeys and chickens that hatched from eggs exposed to slightly cooler temperatures during the final stage of incubation. Turkeys incubated at 32.5 to 34.5°C from day 21 to hatch, either did not grow until the fifth day, or eventually perished because they refused to eat and drink. Davison and Lickiss (1979) found that day-old female chickens exposed to 10°C for 4 hours grew slower for the first 2 weeks. They suggested that the slower growth rate was associated with a depletion of both muscular and hepatic glycogen stores. This hypothesis may also help to explain the slower growth rates of ducklings cooled as embryos in this study. Evidence presented herein indicates that neonate lipid reserves are depleted by egg cooling, but additional research is required to identify precisely (1) the processes involved, (2) the degree to which each affects subsequent growth, and (3) why females appear to be affected more than males.

Differences in the hatch weight of mallard ducklings are fairly small, yet distinct weight classes appear to maintain their relative differences throughout development, although the disparity diminishes with age. The influence of hatch weight on growth is well documented for the young of altricial species (Schifferli 1973, O'Connor 1975, Howe 1976, Järvinen and Ylimaunu 1984, but see Richter 1984), semi-precocial species (Nisbet 1978, Ricklefs et al. 1978), and precocial species (Gardiner 1973, Ankney

1980, Rhymer 1982). In addition to hatch weight, sex has been identified as a factor that influences neonate growth rates. Male ducklings in this study grew faster, on average, than females, and the discrepancy may be related to the slightly larger lipid reserves carried by males. For example, light males and heavy females hatched at the same weight and the growth rates were essentially identical, with the exception that males had a slightly heavier final weight. This suggests that the speed and pattern of early development in the first few weeks post-hatch, may be influenced more by the size of the body reserves than by sex per se. Although the relationship between hatchling size and growth rate is well documented, there is some question as to the mechanism(s) involved.

There are a number of hypotheses to explain the relationship between duckling size and growth rate. The first deals with the size of the yolk sac at hatch. Larger ducklings in this study had proportionately larger yolk sacs than small ducklings, and the difference appeared to manifest itself as a growth rate advantage for at least the first few weeks of development. Deutectomised northern pintail ducklings grew more slowly initially than sham-operated birds with the yolk sac intact (Duncan 1988). Since the yolk sac provides nutrients for early growth and tissue synthesis (Marcstrom 1966, Peach and Thomas 1986, Duncan 1988), ducklings with a larger yolk sac may receive an advantage in growth while learning to feed efficiently. Second, hatch weight differences between conspecifics may represent differences in the developmental stage at hatching (Ricklefs et al. 1978). Larger chicks may differ from others only in being somewhat farther along the normal growth curve of the species. Finally, the allocation of energy to maintenance, activity, and temperature regulation may limit the energy available for growth. This may help explain why the initial growth rate of smaller ducklings in this study was less rapid than for larger conspecifics.

In conclusion, there is an apparent effect of prolonged egg cooling on growth rates of neonate mallards. Cooling duration appears to be more important than

temperature and the adverse effects on growth are more noticeable in females. That these differences appeared in captivity, where conditions were perhaps optimal, means that differences may be even more evident in the wild where ducklings do not have access to a readily available, high quality food source. Any benefit of being a larger mallard duckling at hatch appears to enhance growth early in life. Larger ducklings grew faster, and to a heavier final weight, than small ducklings. Given our present state of knowledge on the subject, the precise reason for this discrepancy is unknown, but the amount of yolk reserves at hatching may be involved.

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IV. THE INFLUENCE OF RADIO BACKPACKS ON WEIGHTS OF FEMALE MALLARDS DURING BROOD REARING: IMPLICATIONS FOR DUCKLING SURVIVAL.

INTRODUCTION

Recent technological developments in radiotelemetry have enabled biologists to document numerous aspects of avian ecology, hitherto impossible without this tool. Concerned with obtaining more accurate estimates of annual recruitment rates, waterfowl biologist in particular have used the technique frequently in attempts to quantify brood survival (Ball et al. 1975, Ringelman and Longcore 1982, Talent et al. 1983, Cowardin et al. 1985, Duncan 1986, Clark et al. 1987, Orthmeyer 1987). The usual procedure involved capturing females, before nesting or during late incubation, and fitting them with a back-mounted radio transmitter similar to that designed by Dwyer (1972). Most investigators assumed that if a backpack were fitted properly to the bird, and there were no obvious changes in its behaviour (i.e., erratic flight), it would adjust to the presence of the radio within a few days (Cowardin et al. 1985, Kirby and Cowardin 1986, Conroy et al. 1989). However, the majority of such studies have ignored a growing body of evidence which showed that birds often did not "adjust" to the discomfort inherent in a radio package and harness (whether backpack or other). Research with waterfowl and a variety of other bird species has documented not only abnormal behaviour (Boag 1972, Greenwood and Sargeant 1973, Gilmer et al 1974, Morris and Black 1980, Perry 1981, Massey et al. 1988, Wanless et al. 1988), but also decreased reproductive success (Lance and Watson 1977, Herzog 1979, Erikstad 1979, Hines and Zwickel 1985, Clark et al. 1987), lower probabilities of survival for the wearer (Gilmer et al. 1974, Warner and Etter 1983, Small and Rusch 1985), and significant weight loss (Schladweiler 1969, Greenwood and Sargeant 1973, Perry 1981).

Studies of the cyclic weight changes in anatids have shown that females experience significant weight losses in the breeding season, particularly during laying and incubation. Losses vary interspecifically, ranging from 23-42%, primarily through depleted lipid reserves (Harris 1970, Korschgen 1977, Ankney and MacInnes 1978, Raveling 1979, Brown 1981, Drobney 1982, Gatti 1983, Ankney 1984, Noyes and Jarvis 1985, Hohman 1986, Murphy and Boag 1989, Barzen and Serie 1990). Lipid stores contribute significantly to egg production and body maintenance so that by the end of incubation most females are in relatively poor body condition, the lowest in their annual cycle (Korschgen 1977, Raveling 1979, Krapu 1981, Ankney 1982, but see Reinecke et al. 1982). This weight loss during reproduction results from physiological stress caused by the succession of significant demands both for egg production and incubation (Ricklefs 1974). The ability of females to cope with additional stressful demands is probably lowest during this period, especially by late incubation, which raises an interesting question: how are the endogenous reserves of a hen affected when the burden of reproduction is complicated by the stress (see Chapter II Results) of being captured and fitted with a radio package?

This study examined the effect of radio backpacks on the weight dynamics of hen mallards, *Anas platyrhynchos*, in captivity. I predicted that fitting a radio transmitter to hens late in incubation would exacerbate normal weight changes. In addition, differences in female body condition at the time of fitting would result in "light" and "heavy" hens responding differently to this added stress.

STUDY AREA AND METHODS

The study was conducted during the summer of 1988 at the Brooks Pheasant Hatchery (Alberta Department of Forestry, Lands and Wildlife) near Brooks, Alberta (50° 35'N, 111°54'W). The conditions in captivity, backpack design, and radio-marking

procedure are described in Chapter II Methods.

Captive female mallards were caught on the 22nd day of incubation and weighed (±10 g) with a Pesola spring scale. Following this initial weighing, hens were weighed weekly for a period of 8 weeks. An additional weight was taken on the day the birds were released to the wild (August 25, 1988). The measurements were used to (1) document changes in hen weight throughout the brood rearing period, (2) determine if there were differences in the rate of weight loss or gain between radio-marked and unmarked birds, and (3) establish whether any of the above variables were influenced by hen body weight at the start of the experiment.

In this study, the body weight of females was considered an adequate measure of physical condition. Numerous studies have shown that body mass and metabolic reserves are positively correlated in waterfowl, and that female weight is a good predictor of reserve status (Harris 1970, Bailey 1979, Raveling 1979, Wishart 1979, Krapu 1981, Ankney 1982, Drobney 1982, Hepp et al. 1987, Serie and Sharp 1989).

Statistical analyses

As a measure of the rate of weight change for each individual, I selected a straight line fitted by linear regression techniques to the weights associated with a period of either continuous loss or gain. The slopes for each period, or segment, were tested with a one-way ANOVA for differences between radio-marked (RAD) and unmarked controls (CON). Pre-hatch weight, brood completion weight, release weight, and absolute weight change from pre-hatch to the time of release were also tested with analysis of variance. All tests followed the procedures in Sokal and Rohlf (1981) and were done using the SPSSx statistical package (SPSS Inc. 1988) with a significance level set at $P<0.05$.

RESULTS

A comparison of body weights of captive female mallards, obtained weekly from day 22 of incubation through the brood rearing period 56 days later, showed that RAD hens (n=18) gained less weight than CON hens (n=18) (Figure IV-1A). These weight changes were divided into two segments for separate analyses: a period of weight loss (A: 0-14 days), and a period of weight gain (B: 14-56 days). Both groups exhibited similar rates of weight loss (one-way ANOVA, $F=0.282$, $p=0.67$), but RAD hens gained weight more slowly than CON hens ($F=5.90$, $p=0.02$). The overall pattern of weekly weight loss and gain was similar in both groups (Figure IV-1B). During this initial period (segment A), RAD hens lost 18.6±5.7 g/week, CON hens 19.6±7.6 g/week, but during the period of weight gain (segment B), RAD hens gained only 9.6±1.7 g/week whereas CON birds gained 17.2±2.8 g/week. This led to a significant difference between groups in absolute weight change, from pre-hatch weight in late incubation to the time of release (August 25). This was also true of the release weights themselves (Table IV-1).

It has been shown that the timing of laying is affected by body condition in winter and spring for female mallards (Krapu 1981, Gatti 1983, Pattenden and Boag 1989). Since there was a considerable range in the date of laying for both RAD and CON hens, I determined whether it was related to body weight by dividing each group into two subgroups (light and heavy) and comparing the weights to timing of events in the reproductive cycle (Appendix IV-1). In order to achieve approximately equal numbers in each subgroup, I used 1000 g as the dividing point between the two groups. The distribution in laying dates and subsequent events in the reproductive cycle were related to body weight and resulted in ca. 1 week's difference in mean hatch dates between the two subgroups. Since all birds were released on the same day they were not at precisely the same stage in their annual weight cycle, because some had completed brood rearing earlier than others.

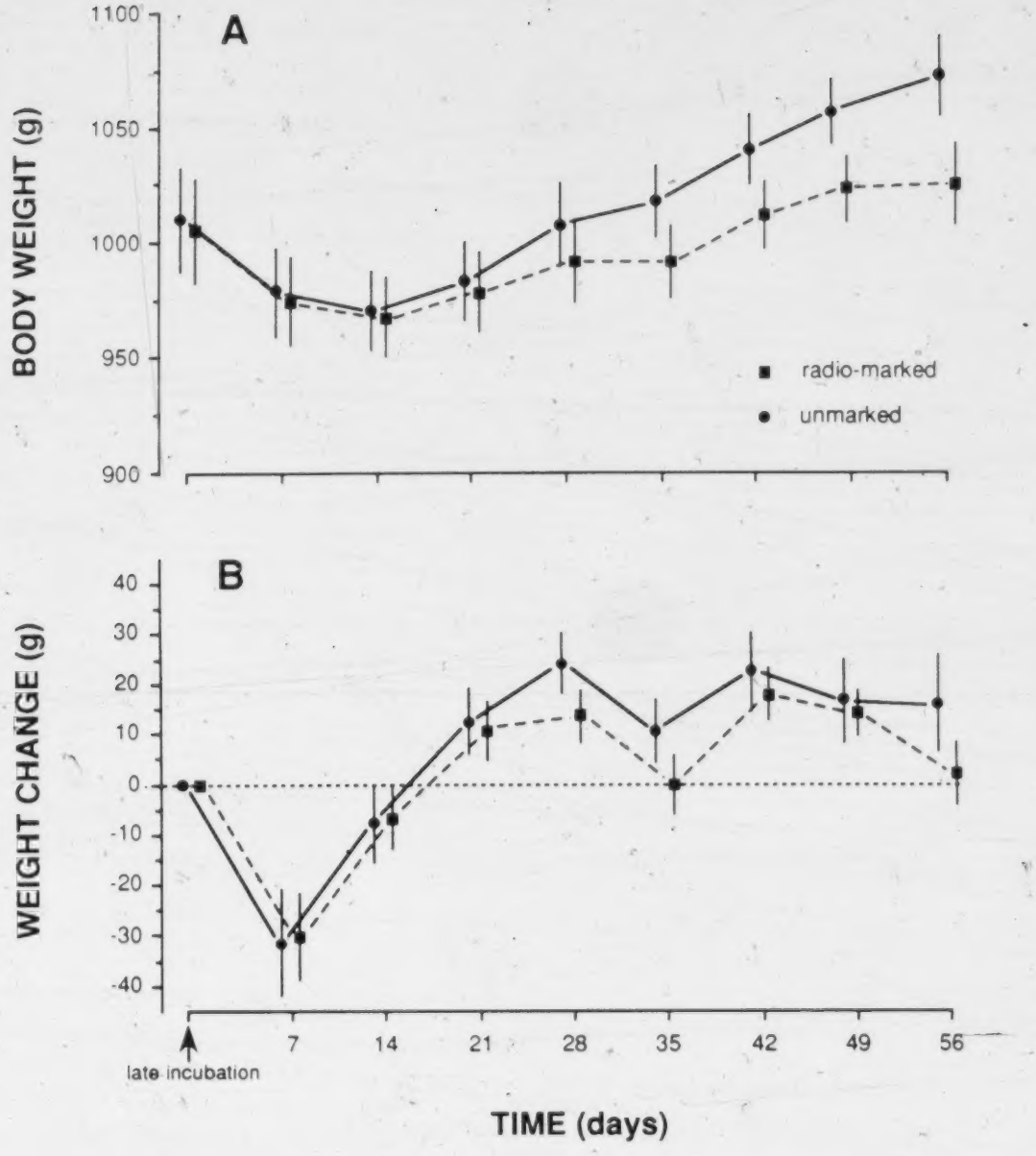

Figure IV-1. Mean weekly body weights (A) and absolute changes (B) for mallard females during brood rearing, either fitted with a radio backpack late in incubation (day 22) or left unmarked. Vertical bars signify standard error

Table IV-1. Mean (±SE) pre- and post-hatch body weights and absolute weight change of captive radio-marked and unmarked female mallards.

Variable	Radio-marked (n=18)	Unmarked (n=18)	P[a]
Hen body weight (g)			
Pre-hatch[b]	1004.4±22.3	1008.6±22.3	0.92
Brood completion[c]	1025.1±17.8	1071.9±21.2	0.10
Release[d]	1035.8±18.7	1111.1±27.2	0.04
Absolute change in weight	31.4±16.3	102.5±21.1	0.02
(%)	(3.3)	(9.2)	

[a] Probability based on a one-way ANOVA.
[b] Weight on the 22nd day of incubation.
[c] Weight at the time the brood had fledged (56 days after pre-hatch weight)
[d] Weight on August 25.

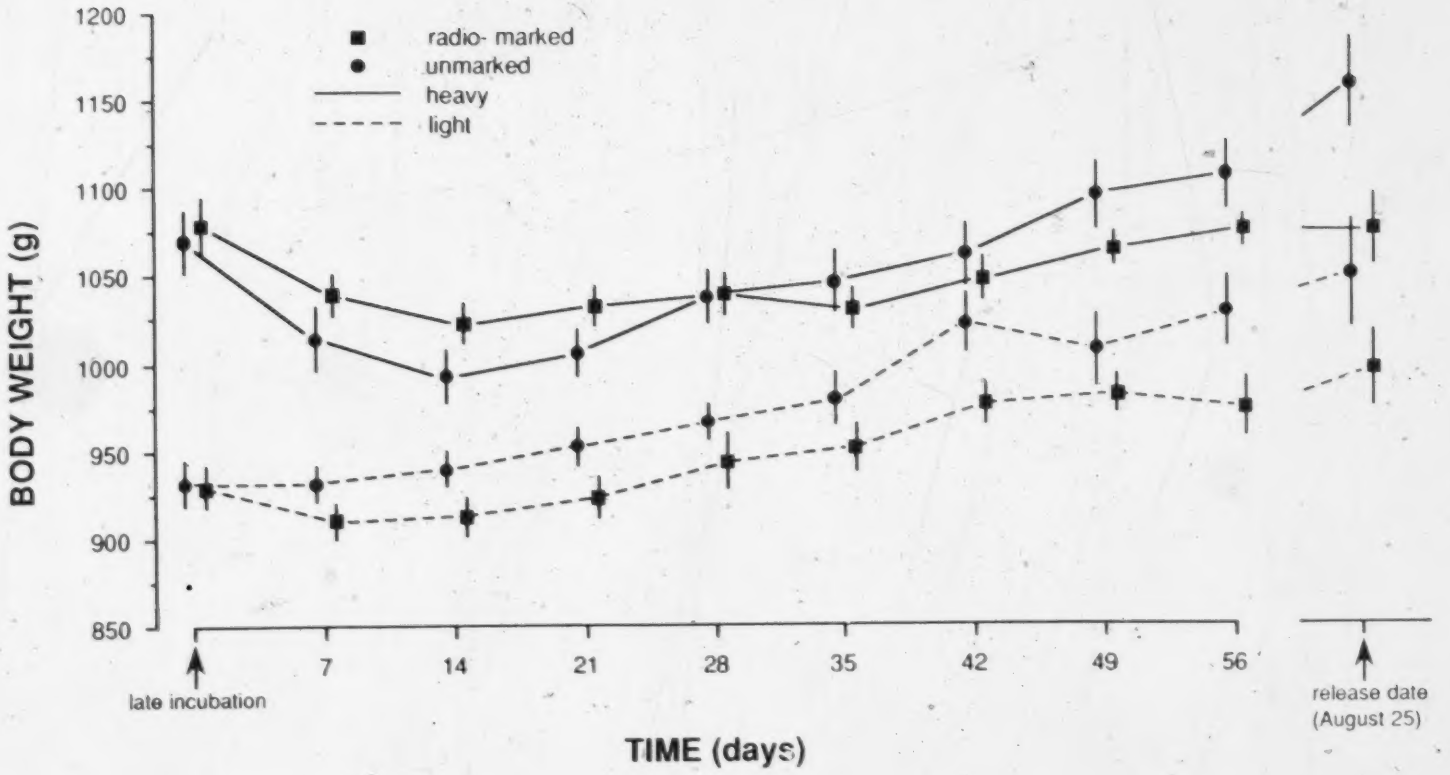

Figure IV-2. Mean body weights for heavy (>1000 g) and light (<1000 g) mallard females during and after brood rearing, either fitted with a radio backpack in late incubation (day 22) or left unmarked. Verticle bars signify standard error.

Table IV-2. Mean (±SE) hatch dates and pre- and post-hatch body weights for light (<1000 g) and heavy (>1000 g) female mallards, either radio-marked or unmarked.

Variable	Light			Heavy		
	Radio-marked (n=9)	Unmarked (n=8)	P[a]	Radio-marked (n=9)	Unmarked (n=10)	P[a]
Hen body weight (g)						
Pre-hatch[b]	929.4±11.3	931.9±13.0	0.91	1079.4±15.7	1070.0±17.1	0.77
Brood completion[c]	975.0±16.8	1028.8±19.7	0.17	1075.1±8.6	1106.5±18.6	0.24
Release[d]	996.1±17.9	1050.6±27.2	0.26	1075.6±14.3	1159.5±21.2	0.04
Absolute change in weight (%)	66.7±14.7 (7.2)	118.7±30.3 (12.7)	0.12	-3.9±25.2 (0.4)	89.5±28.4 (8.4)	0.03

[a] Probability based on a one-way ANOVA.
[b] Weight on the 22nd day of incubation.
[c] Weight at the time the brood had fledged (56 days after pre-hatch weight).
[d] Weight on August 25.

Hens in the RAD group gained less weight than CON hens, regardless of their initial pre-hatch weight (Figure IV-2). On average, hens in the light subgroup began gaining weight by day 7; thus 7-56 days was the segment used for comparing the rates of gain in the two groups. RAD hens weighed significantly less than CON hens after 7 days (one-way ANOVA, $F=14.98$, $p<0.005$), but ANOVA of regression coefficients suggested that the subsequent rate of weight gain in both groups of light females was similar ($F=0.39$, $p=0.58$), (RAD: 9.4 ±2.6 vs CON: 13.8±3.7 g/week). The brood completion weight, release weight, and absolute change over the course of brood rearing were not significantly different for these light weight females (Table IV-2).

Among hens in the heavy subgroup, the rate of weight loss in segment A (0-14 days) was comparable (one-way ANOVA, $F=0.79$, $p=0.31$) for RAD and CON (Figure IV-2). RAD hens lost an average of 28.6±7.1 g/week, while those in the CON group lost 38.5±8.5 g/week. However, the two groups of heavy birds differed significantly ($F=6.77$, $p=0.02$) in the rate of weight gain from 14 to 56 days, with RAD hens gaining less (8.8±2.1 g/week) than CON hens (18.8±3.9 g/week). Both the absolute weight change and final release weight in this group of heavy birds were significantly greater for CON hens than for RAD hens (Table IV-2).

DISCUSSION

Influence of radio backpacks on changes in hen weight

Results of this study showed clearly that the body weight of captive mallard females, overall, continued to decrease after the ducklings hatched. The trend in post-hatch weights followed the same general pattern for both radio-marked and unmarked birds, but those with radios regained weight at a significantly slower rate. This discrepancy resulted in lighter weights for radio-marked females at the completion of brood rearing, and the difference was even more apparent by the end of the summer. The causal relationship found between body weight dynamics and radio backpacks may

be explained either (1) increased energy expenditure caused by elevated preening rates, or (2) more energy loss through disrupted, wet plumage (see Chapter II).

Light and heavy individuals displayed different physiological responses to the presence of the transmitter. Lighter females lost very little body weight immediately following hatch. Instead, they gained steadily for almost the entire brood period, although those with radios gained only half as much as those without. By contrast, heavier females lost greater amounts of weight following hatch, and by the end of the summer RAD hens were significantly lighter than CON hens. This relationship between initial body mass and weight loss has been documented previously for breeding anatids. Although highly variable, weight changes among wood ducks, *Aix sponsa*, were related to the body mass of females in early incubation; heavy birds lost weight at a greater rate than light ones (Harvey et al. 1989). A similar relationship has been found for incubating Canada geese, *Branta canadensis*, (Aldrich and Raveling 1983). Gatti (1983) proposed that heavier (i.e., better body condition) hen mallards could afford to lose more weight than light hens during incubation, and suggested that there is a critical terminal mass, or threshold level, that must be maintained by increasing nutritional intake if necessary (Drent and Daan 1980, Sherry et al. 1980, Gloutney 1989). Both light and heavy radio-marked mallards, however, regained lost body mass at a slower rate than controls, resulting in a substantial body weight difference by the end of brood rearing.

Trends in body weight provide an index to the physiological demands of reproduction, and it is thought that female weights reach an annual minimum at hatch or during the prebasic moult (Weller 1957, Harris 1970, Korschgen 1977, Ankney and MacInnes 1978, Drobney 1980, Ankney and Afton 1988). Such was not the case for mallards in this study; female body weight continued to decline, on average, for a few days post-hatch (Figure IV-1). Similarily, research with diving ducks (Aythyini) has shown that the seasonal minima for breeding females occurred after hatch (Noyes and Jarvis 1985, Hohman 1986). The findings of this study, therefore, appear to contradict the

present understanding of weight dynamics in breeding dabbling ducks, and the timing of a seasonal minima for females. Furthermore, females in this study were given *ad libitum* amounts of high quality ration, and the pattern found here during early brood rearing is very different from that of captive non-breeding mallards (Loesch and Kaminski 1989), those in poor condition have the ability to gain an average of 146 g/week when given a balanced *ad libitum* diet. Therefore, the lack of immediate weight gain by control birds, on average, must be related either to reduced feeding and increased parental care (Rushforth Guinn and Batt 1985), or a programmed anorexia that is dependent upon initial body condition or body size (Sherry et al. 1980, Gaston and Jones 1989), or a combination of both.

Implications for recruitment studies

Biologists have used radiotelemetry extensively in an effort to measure brood survival in waterfowl. Evidence from these studies suggests that total brood loss is often very high among radio-marked hens, although rarely was it implied that the radios were a factor (Ringelman and Longcore 1982, Talent et al. 1983, Duncan 1986, Orthmeyer 1987, Eberhardt et al. 1989, Yarris pers. comm.). Clark et al. (1987) found that radio-marked hens had significantly smaller broods of older ducklings than unmarked hens, and concluded that marked birds produce less young per surviving brood. Research with ducks suggests that by the time of hatch, a female's body condition may influence her ability to raise the brood successfully to fledging. Unmarked northern pintail, *Anas acuta*, hens allocated less time to parental care and more time to self-maintenance activities when their energy reserves were low, thereby creating a potentially lower probability for duckling survival (Rushforth Guinn and Batt 1985). Working with radio-marked mallards, Talent et al. (1983) implied that the physical condition of the hens may have affected their attentiveness towards their broods, while Orthmeyer (1987) found a significant correlation between hen condition and the number of ducklings fledged. It seems possible that the physiological demands of breeding

coupled with the adverse effects of a backpack, as demonstrated in this study, render females less capable of rearing their offspring successfully.

Female body condition may influence duckling survival not only directly through reduced parental care, but perhaps indirectly before or during nesting. The latter situation may arise when hens are fitted with radios prior to nest initiation, possibly interfering with normal weight dynamics during a period critical for accumulating body reserves. Such effects may cause hens to postpone egg laying until later in the season which would postpone hatching, rendering ducklings more susceptable to increased mortality overall, and a lower probability of surviving to fledging (Hill 1984, Eldridge and Krapu 1988). Moreover, females in suboptimal condition may produce eggs of smaller average size. Some studies with waterfowl and other bird species have found a positive correlation between egg size and female condition (Järvinen and Väisänen 1984, Duncan 1987, Hepp et al. 1987, Leblanc 1989). Egg size has been cited as an important reproductive trait because of its positive relationship with survival of the chick (Parsons 1970, Schifferli 1973, O'Connor 1979, Krapu 1979, Ankney 1980, Thomas and Peach Brown 1988, see also Chapter II, but see Leblanc 1987). Finally, female waterfowl in suboptimal breeding condition may lay a clutch, but may possess insufficient metabolic reserves to provide normal incubation. Physiological stress may reduce incubation drive, leading to inattentiveness or abandonment (Harvey 1971, Ankney and MacInnes 1978, Aldrich and Raveling 1983). When this threshold level of body condition is reached, the female is faced with deciding between her own survival or that of her clutch (Ankney and MacInnes 1978, Gloutney 1989). Sayler (pers. comm.) stated that the body condition of radio-marked female mallards and gadwalls, *Anas strepera*, influenced desertion rates, and that this sensitivity is more pronounced later in the nesting season. Furthermore, frequent or prolonged absences from the nest can cause detrimental egg cooling, which ultimately may lead to reduced embryo viability (Prince et al. 1967, Batt and Cornwell 1972, review in Webb 1987), lower neonate survival (see Chapter II), or vulnerability to

potential predation. Thus, the laying date, egg size, and nest attentiveness, dependent upon female body condition, may be altered by radio-marking individuals early in the breeding season.

Implications for female survival

Radio-fitted hens in this study weighed noticeably less than control hens at the end of the summer. If radio backpacks are not designed to fall off soon after brood rearing, the suboptimal condition of those individuals so fitted may, at the very least, create a lag in the timing of events to follow in the annual cycle, or at the other extreme, place their lives at risk. For example,radio-marked females may experience a delay in the feather moults that take place before or during fall migration. Before pre-migratory fattening occurs the birds must bear the energetic cost of growing new flight feathers, while at the same time rearing a brood. For wild mallards, this period usually lasts 30 days, during which they experience a noticeable drain on metabolic reserves (Pehrsson 1987, Panek and Majewski 1990). In fact, the rate of feather regrowth appears to be related to the initial body condition (Panek and Majewski 1990). Shortly after the remex moult, female mallards initiate the prealternate moult while on northern staging areas, and complete it during the fall migration or on wintering areas (Young and Boag 1981, Heitmeyer 1987). Protein and energy requirements increase greatly during both moult and migration (Blem 1980, Heitmeyer 1988a, 1988b). Females in poor post-breeding condition may be unable to acquire sufficient reserves to sustain lengthy migration southward. Owen (1970) stated that pre-migratory fattening was essential for blue-winged teal, *Anas discors*. Similarily, Serie and Sharp (1989) demonstrated that canvasbacks, *Aythya valisineria*, require large fat reserves for migration, and the size of these reserves was the principal factor controlling lengths of stopovers. Finally, body reserve levels appear to be related to over-winter survival. Work with mallards (Hepp et al. 1986) and canvasbacks (Haramis et al. 1986) has demonstrated that adults with a lower body mass in fall and winter have lower

probabilities of survival, primarily through their greater vulnerability to hunting mortality. Similar results were obtained for black ducks, *Anas rubripes*, for which it was implied that survival estimates may have been influenced by the radio backpacks carried by the birds (Conroy et al. 1989). It is also reasonable to assume that building and maintaining fat reserves during fall migration may have some survival value during the winter (Reinecke et al. 1982). Furthermore, events in the annual cycle discussed above are intertwined and, as Heitmeyer (1988b: 676) stated, "initiation and efficient completion of these events may be partly controlled by availability of nutrients and subsequent storage of reseves." Therefore, radio-marking mallard hens during the breeding season may influence directly their ability to obtain energy reserves necessary for surviving a succession of energetically costly events, both during and following brood rearing.

Alternatives to current techniques

The results of this study suggest that the use of radio backpacks on hens to quantify brood survival may lead to biased conclusions. This is realized simply by the fact that radio backpacks affect the status of endogenous reserves, and reserve status is inextricably connected with many behavioural factors. If this bias were to be quantified, perhaps then the apparently equivocal results obtained could be interpreted with more confidence. Modifications to existing procedures might require that researchers obtain a condition index of the birds being fitted, and determine its relationship to brood survival. This factor could be taken into account when the results are tabulated, while at the same time acknowledging that the behaviour and experience of individual hens can play an important modifying role. Another alternative involves incorporating a "weak link" into the harness design as a break-away mechanism (Karl and Clout 1987). Were the backpack to fall off shortly after brood rearing, it would reduce the threat to a female's own subsequent survival and reproductive fitness. Modifications notwithstanding, perhaps the most effective means of dealing with this problem is to avoid the use of external mounted radio transmitters on waterfowl, at least until a more

compatable design is developed (Giroux et al. 1990). Implantable radio transmitters have been tested on ducks, but the application has met with only limited success (Korschgen et al. 1984). The use of nasal markers to identify females, or web-tagging juveniles, may be more cost effective methods of quantifying recruitment, by providing more reliable estimates of duckling mortality (Lokemoen et al. 1990).

In conclusion, radio backpacks had a significant measureable effect on the body condition of female mallards during brood rearing. Both light and heavy hens with radios weighed substantially less than control birds in their respective group at the end of the summer. A review of other studies confirmed that physical condition is crucial to the reproductive success of female waterfowl. Therefore, using radiotelemetry to quantify duckling survival forces a hen to carry a radio package through a period critical to both herself and her offspring. Caution is advised when recruitment estimates are obtained by using radio-marked hens; duckling mortality estimates may be inflated artificially. Given the potential problems inherent in the present techniques, I suggest that alternative methods be given serious consideration.

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V. CONCLUDING DISCUSSION

This study documented some actual and potential problems inherent in attaching radio transmitters to female mallards during the breeding season. I investigated incubation constancy, egg temperatures and hatching success of radio-marked hens in the wild. Using captive birds, I determined the relationship between prolonged egg cooling and subsequent neonate body reserves, survival, and growth. Finally, I investigated the stress to hen mallards of wearing a radio backpack, specifically its impact on the physical condition of the hen during brood rearing.

Hatching success in the wild and under the captive conditions of this study were both very good (>90%). Duckling survival in the wild was unknown but under captive conditions was also good (>90%). As a result, I was unable to demonstrate that radio-marked females hatched fewer eggs per clutch or fledged fewer ducklings under captive conditions. Had climatological conditions been less favourable, the longer absences recorded for radio-marked hens would have resulted in more severe egg cooling, which could have reduced the hatching success of mallard eggs (Prince et al. 1969, Batt and Cornwell 1972). Nevertheless, the viability of mallard embryos themselves appeared little affected by prolonged exposures to moderate cooling temperatures.

Although duckling mortality in captivity was low, the viability of young was apparently influenced by hatch weight and indirectly by embryonic cooling; heavy ducklings from eggs incubated naturally survived better than light ones from eggs cooled experimentally. There are two possible explanations for this relationship. First, larger hatchlings possess more body reserves and, perhaps more importantly, proportionately larger yolk sacs than smaller hatchlings. For many bird species, survival advantage is attributed to those conspecifics hatching with a bigger body size (Schifferli 1973, Ricklefs et al. 1978), more metabolic reserves (Krapu 1979, Ankney 1980, Thomas and

Peach Brown 1988), or a larger yolk sac (Coulson et al. 1969, Parsons 1970, Birkhead 1985). Additional evidence supporting the relationship between size and survival exists for snow geese, *Anser caerulescens*, (Ankney 1980) and red grouse, *Lagopus lagopus scoticus*, (Moss et al. 1981) held under "optimal" captive conditions, similar to this study. Second, prolonged egg cooling may reduce the level of body reserves in the neonate, presumably as a result of increased metabolic demands on the embryo (Boersma and Wheelwright 1979, Whittow 1986). Few data exist on the long-term physiological effects of sublethal exposure of embryos to thermal stress. However, data from this study indicated that lipid reserves and yolk sac size were depleted when eggs were cooled, and that the body tissues of the neonates which subsequently hatched contained a higher proportion of water, linked with lesser developmental maturity (Ricklefs 1979), probably metabolic water resulting from metabolism of lipids.

Most of the differences in the variables compared between ducklings from cooled and uncooled eggs were not statistically significant. Nevertheless, given the small sample size of neonate mallards, and the consistency of trends, these differences may be biologically meaningful. For example, many composition variables of neonates from cooled eggs changed in a consistent manner. Liver lipids decreased with increased duration of egg cooling, as did yolk sac size, lipid, and water content; water content of the whole duckling increased, while the lipid fraction decreased with the severity of exposure. These trends led me to conclude that the body reserves of smaller ducklings, normally less than larger ducklings to begin with, are reduced further by the effects of prolonged embryonic cooling. Although these effects are felt by all 22-day-old embryos, regardless of size, smaller embryos may be less capable of enduring the thermal stress, either retarding functional development or reducing the probability of their survival.

Although duckling mortality in captivity was lower than that expected in the wild (Talent et al. 1983, Clark et al. 1987, Orthmeyer 1987), it assumed the same pattern

(majority dying in the first week post-hatch). Many different factors have been implicated in early losses of wild mallard ducklings, but most often predation is cited as the principal cause (Sargeant et al. 1973, Talent et al. 1983, Cowardin et al. 1985); yet little evidence to supports this hypothesis. As demonstrated by the results of this study, given "optimal" conditions of food, water, and shelter and the absence of most selective forces normally encountered in the wild, duckling losses still occurred early in life. Individuals that perished during this study were much lighter than their cohorts at the time of death (Appendix II-1), as though they had fed very little or were somehow weakened. Other research with dabbling ducks has suggested that considerable mortality was the result of congenital weakness (Keith 1961), exposure to the elements (Titman and Lowther 1975), and starvation (Duncan 1986). All this suggests that a high proportion of duckling mortality, normally attributed to predation, may result from the combined effects of other factors acting on the embryo in the egg, and on the duckling shortly after hatching.

Duckling growth was another post-hatch variable influenced by embryonic cooling and hatchling size. Ducklings (especially females) from experimentally cooled eggs grew at a slower rate, and to a slightly lighter fledging weight, than those from eggs incubated naturally. These differences may be explained by (1) a portion of the body reserves normally used for early growth being diverted to fuel embryonic thermogenesis and maintenance as a result of prolonged cooling, and/or (2) less developmentally mature body tissues at hatching. In relation to body size alone, growth rates of mallard ducklings were consistent with those reported by Rhymer (1982); larger individuals grew faster and fledged at heavier weights than smaller ones. Larger ducklings in this study had proportionately larger yolk sacs, perhaps leading to an early growth advantage since the yolk sac provides nutrients for early growth and tissue synthesis (Marcström 1966, Peach and Thomas 1986, Duncan 1988). Also, hatch weight differences between conspecifics may represent differences in the developmental stage

at hatching, with larger chicks being somewhat farther along the normal growth curve of the species (Ricklefs et al. 1978). Finally, the allocation of energy to early post-hatch maintenance, activity, and temperature regulation may limit the energy available for growth, especially for smaller individuals.

The behaviour of female mallards is unequivocally altered when they are fitted with a radio backpack late in incubation. The most obvious changes in behaviour were increased preening and less time on the water. Both groups of captive hens were apparently able to meet the energetic demands of early brood rearing by feeding very little (ca. 2%). This contrasts with 57% for wild mottled ducks, *Anas fulvigula maculosa*, (Paulus 1984) and 47% for northern pintails, *A. acuta*, (Rushforth Guinn and Batt 1985), neither of which were feeding on commercial duck food. Mottled ducks and pintails also spent far less time in alert behaviour while leading very young broods (13% and 10%, respectively), compared with 22% for captive mallards in this study. Even while their ducklings were very young, wild ducks spent more time in self-maintenance than parental care activities. Captive birds, on the other hand, were fed *ad libitum* ,enabling them to allocate less time to feeding but more time to the care of their broods. I suggest that the difference in time spent feeding (less for radioed hens) would be magnified in the field, simply because wild birds apparently must feed much more to meet their nutritional requirements. To complicate matters, a partial avoidance of water would exacerbate this problem for radio-marked hens, especially as all dabbling ducks seek refuge and the majority of their food on the water. These behavioural changes are themselves reason enough to be cautious when interpreting the results of brood survival studies using radio-marked females.

Data from captive mallards demonstrated that those wearing transmitters gained less weight than controls after their broods hatched. Assuming that wearing transmitters would have the same negative impact on wild mallards, it may cause such hens to become less attentive to their broods. Individuals that exhausted their metabolic reserves

by the time of hatch would be expected to devote more than the normal fraction of time to feeding as their body condition approached a critical level (Rushforth Guinn and Batt 1985). Should this occur, the probability of duckling survival to fledging would logically be lowered. In addition to the possibility of lowered offspring survival, the negative impact of backpack transmitters on female body condition places radioed hens at a physiological disadvantage before the demands of flight-feather moult, pre-migratory fattening, and prealternate moult. These events are at least partially dependent upon female body condition. If the suboptimal condition were to persist into the winter, a bird's future reproductive success (Gates and Woehler 1968, Reinecke et al. 1982, Porter et al. 1983, Pattenden and Boag 1989) or survival (Warner and Etter 1985, Hepp et al. 1986, Haramis et al. 1986, Conroy et al. 1989) may be impaired.

It is not always possible to observe behavioural and physiological changes among ducks radio-marked in the field. Thus, the often invoked assumption of "no apparent impact" may be invalid. Data presented here demonstrated that there are several subtle ways in which a radio backpack can influence a female's ability to reproduce successfully. For researchers using backpacks to measure duckling recruitment, the combined total of these subtle effects translates into a major problem when radio-marking is used for wild birds; the well-being of both the hen and her ducklings is affected. Thus, those incorporating radiotelemetry into the study of waterfowl ecology, or that of other birds, should not ignore the problems that can arise when these birds are forced to carry a transmitter, and should be aware of alternative transmitter designs. If the effects of a transmitter are unknown, or cannot be qualified fully, the results should be interpreted with great caution.

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Appendix I. Age and weight (mean±SE) at time of death for captive mallard ducklings found dead in their pens as compared to those brood members that survived.

Sex	Age	Body weight (g) Dead	Alive	P
Male	2	30.86±1.14 (6)	32.68±0.58 (60)	0.35[a]
	4	27.94±0.53 (10)	43.23±0.99 (60)	<0.001[b]
	6	29.00±0.58 (3)	63.82±1.58 (60)	<0.001[b]
Female	2	30.13±1.27 (6)	33.56±0.56 (55)	0.07[a]
	4	28.30±0.90 (8)	43.95±1.00 (55)	<0.001[b]

[a] Probability based on a one-way ANOVA.
[b] Probability based on an unpaired *t*-test for heterogeneous variances.

Appendix II. Chronological timing (mean±SE) of events during the breeding season for light (<1000 g) and heavy (>1000 g) female mallards in captivity, either radio-marked or unmarked.

Variable	Light			Heavy		
	Radio-marked (n=9)	Unmarked (n=8)	P[a]	Radio-marked (n=9)	Unmarked (n=10)	P[a]
Nest initiation[b] (range)	7.8±1.7 (May 3-15)	10.1±3.2 (April 29-May 30)	0.43	1.4±1.6 (April 27-May 12)	3.8±1.5 (April 28-May 11)	0.39
Mean June hatch date (range)	11.9±2.1 (5-22)	13.4±3.5 (1-30)	0.63	5.8±2.2 (1-21)	8.1±1.9 (3-23)	0.44
No. days to release[c] (range)	76.9±2.3 (65-83)	75.8±4.1 (58-92)	0.79	84.8±2.3 (69-92)	82.2±2.4 (65-90)	0.61

[a] Probability based on a one-way ANOVA.

[b] Mean June date on which the first egg was laid.

[c] Total time span between late incubation (day 22) and the day the birds were released to the wild.